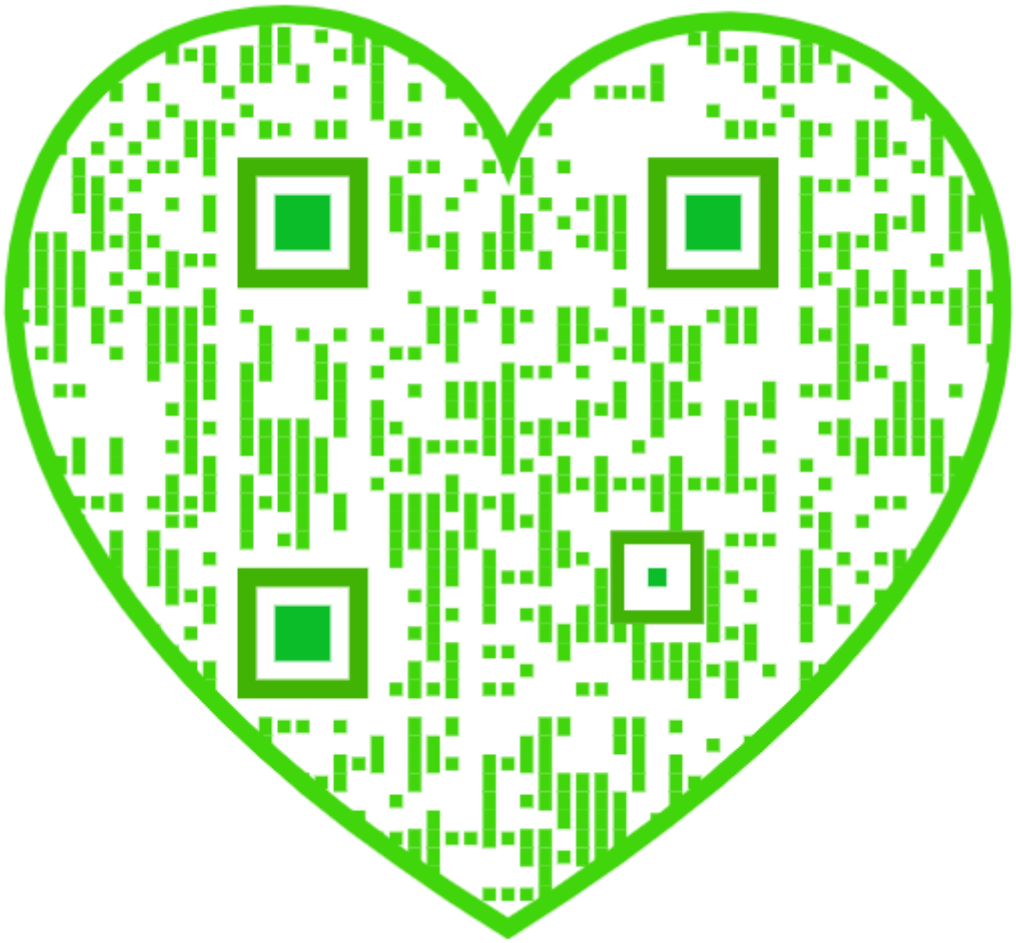


STRASBURGER'S
TEXT-BOOK OF BOTANY

MACMILLAN AND CO., LIMITED
LONDON • BOMBAY • CALCUTTA • MADRAS
MELBOURNE

THE MACMILLAN COMPANY
NEW YORK • BOSTON • CHICAGO
DALLAS • SAN FRANCISCO

THE MACMILLAN CO. OF CANADA, LTD.
TORONTO

STRASBURGER'S
TEXT-BOOK OF BOTANY

RE-WRITTEN BY

DR. HANS FITTING
PROFESSOR IN THE UNIVERSITY OF BONN

DR. LUDWIG JOST
PROFESSOR IN THE UNIVERSITY OF HEIDELBERG

DR. HEINRICH SCHENCK
PROFESSOR IN THE TECHNICAL ACADEMY OF DARMSTADT

DR. GEORGE KARSTEN
PROFESSOR IN THE UNIVERSITY OF HALLE/SAALE

FIFTH ENGLISH EDITION

REVISED WITH THE FOURTEENTH GERMAN EDITION BY

W. H. LANG, M.B., D.Sc., F.R.S.
BARKER PROFESSOR OF CRYPTOGAMIC BOTANY IN THE UNIVERSITY OF MANCHESTER

WITH 833 ILLUSTRATIONS, IN PART COLOURED

MACMILLAN AND CO., LIMITED
ST. MARTIN'S STREET, LONDON
1921

FORESTRY

COPYRIGHT

First English Edition, 1898
Second English Edition, 1903
Third English Edition, 1908
Fourth English Edition, 1912
Fifth English Edition, 1921

AGRIC. DEPT. Forestry

PREFATORY NOTE

THE original authors of this text-book as it appeared in 1894 were Professors Eduard Strasburger, Fritz Noll, Heinrich Schenck, and A. F. W. Schimper. The death of Professor Strasburger since the last English edition was published renders it inaccurate to give his name as an author of the work. His position as the original founder of the text-book requires to be recorded and is therefore indicated by the name Strasburger's Text-Book, which has been in current use in this country. In the present edition the division on Morphology is by Professor Fitting, that on Physiology by Professor Jost, that on Thallophyta, Bryophyta, and Pteridophyta by Professor Schenck, and that on Spermatophyta by Professor Karsten. Their names are therefore given as the authors on the title-page.

The first edition of the English translation was the work of Dr. H. C. Porter, Assistant Instructor of Botany, University of Pennsylvania. The proofs of this edition were revised by Professor Seward, M.A., F.R.S. The second English edition was based upon Dr. Porter's translation, which was revised with the fifth German edition. The third English edition was revised with the eighth German edition, and the fourth English edition with the tenth German edition. The present edition has been similarly revised throughout with the fourteenth German edition. Such extensive changes, including the substitution of completely new sections on Morphology, Physiology, and Spermatophyta, have, however, been made in the work since it was first translated that it seems advisable to give in outline the history of the

481250

English translation instead of retaining Dr. Porter's name on the title-page.

The official plants mentioned under the Natural Orders are those of the British Pharmacopoeia instead of those official in Germany, Switzerland, and Austria, which are given in the original.

WILLIAM H. LANG.

MANCHESTER, 1921.

CONTENTS

PAGE

INTRODUCTION 1

PART I. GENERAL BOTANY

DIVISION I. MORPHOLOGY

SECTION I. CYTOLOGY

I. Form and Size of Cells 10
II. The Living Cell Contents. The Protoplast 11
A. The constituent parts of the cell 11
B. Main vital phenomena of protoplasts 13
C. Chemical properties of the protoplast 14
D. Structure of the parts of the protoplast 15
E. Origin of the elements of the protoplast 21
III. The Larger Non-living Inclusions of the Protoplasts . . . 27
IV. The Cell Wall 34

SECTION II. HISTOLOGY

I. The Formation of Tissues 40
II. Kinds of Cells, Tissues, and Tissue-systems 45
A. The formative tissues 46
B. The permanent tissues 47

SECTION III. ORGANOGRAPHY

I. Vegetative Organs 73
A. The Thallus 73
B. The Cormus 83
1. Construction of the Typical Cormus 84
(α) The shoot 84
(α) The growing point 84
(β) The axis of the shoot 87
(γ) The leaves 106
(δ) The branching of the shoot 119

PAGE

(*b*) The root 131
(*c*) Secondary growth in thickness of the cormus . . 140
2. Adaptations of the Cormus to its Mode of Life and to the Environment 165
A. Autotrophic cormophytes 165
(*a*) Adaptations to the humidity of the environment . . 165
(*b*) Adaptations for obtaining light 181
(*c*) Adaptations of green cormophytes to special modes of nutrition 185
B. Heterotrophic cormophytes 188
II. Organs of Reproduction 192

SECTION IV. THE THEORY OF DESCENT AND THE ORIGIN OF NEW SPECIES

A. The theory of descent 206
B. Formation of species and the origin of adaptations 210

DIVISION II. PHYSIOLOGY

Essential phenomena of life 215

SECTION I. METABOLISM

I. The Chemical Composition of the Plant 220
II. The Nutrient Substances; their Absorption and their Movement within the Plant 222
III. The Assimilation of the Food Materials 247
IV. Translocation and Transformation of Assimilates . . . 263
V. Respiration and Fermentation 269

SECTION II. DEVELOPMENT

I. Introductory Remarks 278
1. The measurement of growth 278
2. The phases of growth 282
II. The Factors of Development 288
A. External factors 288
B. Internal factors 296
III. The Course of Development and its Dependence on External and Internal Factors 301
A. Resting condition and the commencement of growth . . 303
B. Growth and cell division 306
C. Further periodic changes in vegetative form . . . 307
D. Duration of life 309
E. Reproduction 310
F. Heredity, variability, origin of species 316

SECTION III. MOVEMENT

PAGE

I. Movements of Locomotion 327
II. Movements of Curvature 332
A. Hygroscopic movements 333
B. Movements of curvature in the living plant 335
1. Autonomic movements of curvature 335
2. Paratonic movements 337
(*a*) Tropisms 338
(*b*) Nastic movements 356

PART II. SPECIAL BOTANY

DIVISION I. THALLOPHYTA. BRYOPHYTA. PTERIDOPHYAT

THALLOPHYTA 367
Bacteria 370
Cyanophyceae 376
Flagellata 378
Myxomycetes 381
Dinoflagellatae 386
Diatomeae 387
Conjugatae 392
Heterocontae 396
Chlorophyceae 398
Phaeophyceae 409
Characeae 418
Rhodophyceae 421
Phycomycetes 428
Eumycetes 436
Lichenes 469
BRYOPHYTA 475
Hepaticae 483
Musci 489
PTERIDOPHYTA 496
Filicinae 503
Equisetinae 517
Sphenophyllinae 522
Lycopodinae 523
Pteridospermeae 534

DIVISION II. SPERMATOPHYTA

The Transition from the Pteridophyta to the Spermatophyta . . . 539
Scheme of Alternation of Generations 543

PAGE

Morphology and Ecology of the Flower 544
1. Morphology 544
Gymnosperms 544
Angiosperms 545
2. Ecology 551
Development of the Sexual Generation 561
A. Gymnosperms 561
(*a*) Cycadeae and Ginkgo 562
(*b*) Coniferae 566
(*c*) Gnetinae 569
B. Angiosperms 570
The seed 579
The fruit 582
Distribution of seeds 584
Germination 587
Arrangement of the Classes, Orders, and Families 589
I. GYMNOSPERMAE 589
Cycadinae 589
Ginkgoinae 591
Coniferae 592
Gnetinae 602
FOSSIL GYMNOSPERMS 604
II. ANGIOSPERMAE 606
DICOTYLAE 608
CHORIPETALAE 609
MONOCHLAMYDEAE 609
Juglandiflorae 609
Querciflorae 609
Saliciflorae 614
Urticinae 616
Loranthiflorae 620
Polygoninae 621
Piperinae 621
Hamamelidinae 623
Tricoccae 623
Centrospermae 627
DIALYPETALAE 629
Polycarpicae 629
Rhoeadinae 639
Cistiflorae 646
Columniferae 647
Gruinales 651
Sapindinae 655
Frangulinae 657

PAGE

Rosiflorae 658
Leguminosae 664
Myrtiflorae 673
Umbelliflorae 677
SYMPETALAE 684
PENTACYCLICAE 684
Ericinae 684
Diospyrinae 686
Primulinae 687
TETRACYCLICAE 687
(*a*) *Ovary superior*—
Contortae 687
Tubiflorae 690
Personatae 696
(*b*) *Ovary inferior*—
Rubiinae 704
Synandrae 707
MONOCOTYLAE 718
(*a*) *Flowers actinomorphic*—
Helobiae 719
Liliiflorae 721
Enantioblastae 730
(*b*) *Flowers more or less reduced*—
Glumiflorae 730
Spadiciflorae 737
(*c*) *Flowers zygomorphic*—
Scitamineae 742
Gynandrae 745
FOSSIL ANGIOSPERMS 749

INDEX OF LITERATURE 751

SYSTEMATIC INDEX OF THE OFFICIAL AND POISONOUS PLANTS . . 773

INDEX 777

INTRODUCTION

ORGANISMS are customarily distinguished as animals and plants and a corresponding division of Biology, which treats of living beings generally, is made into the sciences of Zoology and Botany.

The green, attached, flowering, and fruiting organisms are distinguished as plants in contrast to animals, which are usually capable of free movements and seek, capture, and devour their food. Easy as it appears on a superficial acquaintance to draw the boundary between the vegetable and animal kingdoms, it is really very difficult. In the case of those very simply constructed organisms with little external or internal differentiation, which are usually regarded as lowest in the scale, all distinguishing characteristics may fail us. The following important properties are in fact common to both animals and plants:

1. Plants and animals both consist of one or many microscopically small cells, which increase in number by a process of division. They have thus a FUNDAMENTALLY SIMILAR INTERNAL STRUCTURE.

2. Plants and animals are living beings and AGREE IN THEIR MOST IMPORTANT VITAL PROCESSES. The processes of nutrition and of reproduction, of growth and of development, are, broadly considered, essentially similar in animals and plants. A plant also respires with the production of heat, and exhibits powers of movement and irritability of various kinds.

3. This profound agreement in the manifestations of life in plants and animals becomes less surprising when it is realised that THE LIFE OF BOTH IS ASSOCIATED WITH A VERY SIMILAR UNDERLYING SUBSTANCE, THE PROTOPLASM OF THE CELLS.

These and many other facts indicate that plants are really related among themselves and to the animals. This assumption of a GENETIC RELATIONSHIP finds its expression in the THEORY OF DESCENT which may be regarded as the fundamental biological theory. The idea of a gradual evolution of higher organisms from lower was familiar to the Greek philosophers, but a scientific basis was first given to this hypothesis in the last century. It was especially through the work of CHARLES DARWIN ([1]), who accumulated evidence for a reconsideration

of the whole problem of organic evolution, that the belief in the immutability of species was finally destroyed. From the study of the fossil remains and impressions of animals and plants it has been established that in earlier geological periods forms of life differing from those of the present age existed on the earth. It is also generally assumed that all living animals and plants have been derived by gradual modification from previously existing forms. This leads to the further conclusion that those organisms possessing closely similar structure, which are united as species in a genus, are in reality related to one another. It is also probable that the union of corresponding genera into one family and of families into higher groups in a "natural" system serves to give expression to a real relationship existing between them. The evolutionary developments, *i.e.* the transformations which an organism has undergone in its past generations, were termed its PHYLOGENY by ERNST HAECKEL (2). The development or series of changes passed through by the individual in attaining the adult condition he distinguished as the ONTOGENY. It is assumed on the theory of descent that the more highly organised plants and animals had their phylogenetic origin in forms which perhaps resembled the simplest still existing. The phylogenetic development proceeded from these, on the one hand in the direction of the higher animals, and on the other in the direction of well-defined plants. On this assumption, which is supported by the properties which animals and plants have in common and by the impossibility of drawing a sharp line between animal and plant in the lowest groups, all living beings form one NATURAL KINGDOM.

The following may be mentioned as distinctly marked characteristics of plants. The external development of the important surface of the body, which serves to absorb the food in plants, contrasts with the internal body surface to which the mouth gives entrance in the animal. The investing walls of vegetable cells are already represented in certain series of lower organisms which afford the probable starting-point for the phylogenetic development of plants. Lastly, the green chromatophores of plant-cells are characteristic. By means of the green colouring matter, plants have the power of producing their own nutritive substances from certain constituents of the air and water, and from the salts contained in the soil, and are thus able to exist independently; while animals are dependent, directly or indirectly, for their nourishment, and so for their very existence, on plants. Almost all the other differences which distinguish plants from animals may be traced to the manner in which they obtain their food. Another characteristic of plants is the unlimited duration of their ontogenetic development, which is continuous at the growing points during their whole life. That none of these criteria are alone sufficient for distinguishing plants from animals is evident from the fact that all the Fungi are devoid of green pigment, and, like animals,

are dependent on substances produced by green plants for their nourishment. On the borderland of the two kingdoms, where all other distinctions are wanting, phylogenetic resemblances, according as they may indicate a probable relationship with plants or animals, serve as a guide in determining the position of an organism.

While it is thus impossible to give any strict definition of a "plant" which will sharply separate plants from animals, a distinction between organisms and non-living bodies is more easy. We know no living being in which protoplasm is wanting, while active protoplasm is not to be demonstrated in any lifeless body. Since in the sphere of organic chemistry sugars have been synthesised by EMIL FISCHER and the way towards the synthesis of proteids opened up, there is increased justification for the assumption that the protoplasm forming the starting-point of organic development had an inorganic origin. In ancient times such a "spontaneous generation" was regarded as a possibility even for highly organised animals and plants. It was a widely-spread opinion, shared in by ARISTOTLE himself, that such living beings could originate from mud and sand. It is now known from repeated experiments that even the most minute and simplest organisms with which we are acquainted do not arise in this way but only proceed from their like. Living substance may, however, have arisen from non-living at some stage in the development of the earth or of another planet when the special conditions required for its formation occurred. In order that the organic world should have proceeded from this first living substance, the latter must from the beginning have been able to maintain itself, to grow, and to transform matter taken up from without into its own substance. It must also have been capable of reproduction, *i.e.* of multiplying by separation into a number of parts, and further of acquiring new and inheritable properties. In short, this original living substance must have already possessed all the characteristics of life.

Botany may be divided into a number of parts. MORPHOLOGY is concerned with the recognition and understanding of the external form and internal structure of plants and of their ontogenetic development. PHYSIOLOGY investigates the vital phenomena of plants. Both morphology and physiology take into consideration the relation of plants to the environment and the external conditions, and endeavour to ascertain whether and how far the structure and the special physiology of each plant can be regarded as adaptations to the peculiarities of its environment. These parts of morphology and physiology are often separated from the rest under the name ECOLOGY. SYSTEMATIC BOTANY deals with the description of the kinds of plants and with the classification of the vegetable kingdom. The GEOGRAPHY OF PLANTS has as its objects to determine the distribution of plants

on the surface of the earth and to elucidate the causes of this. Extinct plants and the succession of plants in time form the subject matter of PALAEOPHYTOLOGY, which is thus the historical study of the changes which have taken place in the vegetation of the earth. All these are subdivisions of PURE or THEORETICAL botany.

Botany does not, however, pursue theoretical aims only; it is also concerned with rendering the knowledge so obtained useful to mankind. For instance, accurate information is obtained regarding plants of economic value and how to better employ these, and adulterations of substances of vegetable origin are detected. There have thus to be added to the divisions of pure botany the numerous branches of APPLIED BOTANY, *e.g.* the study of medicinal plants and drugs, of vegetable food-substances, of technically valuable plants and their products, agricultural botany, and that part of plant pathology which is concerned with the prevention and treatment of diseases of plants.

In this work, which is primarily concerned with pure botany, a division is made into a general and a special part. The object of GENERAL BOTANY is, by well-devised experiments and by comparison, to ascertain the most distinctive properties of plants in general or of the main groups. General botany is further divided into the two sections treating of morphology and physiology.

The object of SPECIAL BOTANY is to describe the structural features, the methods of reproduction, and the modes of life of the various groups of plants. It attempts also to express the more or less close relationships which exist between plants by arranging them in as "natural" a system as possible. In this special part a few main facts as to some branches of applied botany, especially regarding pharmaceutical plants, are inserted. The results of palaeophytological study are placed in relation to the description of the particular groups of existing plants. Lastly, the geography of plants is touched on, though no connected account of it is attempted.

PART I

GENERAL BOTANY

DIVISION I

MORPHOLOGY

GENERAL BOTANY

DIVISION I

MORPHOLOGY

MORPHOLOGY is the study of the external form and the internal structure of plants and the ontogenetic development of the plant body as a whole and of its members. In seeking to establish the significance and the phylogenetic origin of the parts of plants and the causes of the formative processes, it aims at a scientific understanding of the forms of plants.

1. The outer and inner construction of a living being can only be understood when it is clearly realised that the animal or plant is a living ORGANISM, *i.e.* a structure the main parts of which are not meaningless appendages or members, but necessary ORGANS by the harmonious co-operation of which the life of the whole is carried on. Almost all the external parts of plants, and of animals also, are such organs performing definite functions. They can, however, only play their parts in the service of the whole organism when they are appropriately constructed, or, in other words, when their structure corresponds with or is adapted to their functions. Since the various parts of the higher plants have diverse functions, it is easy to see why the plant is composed of members very unlike in form and structure.

In order to fully understand the construction of an organism it is further necessary to know the conditions under which it lives and to be acquainted with its environment. Every plant, or animal, has structural peculiarities which enable it to live only under certain conditions of life which are not provided everywhere on the earth's surface. The conditions of life, for example, are very different in water from those in a desert, and water plants and desert plants are very differently constructed. They can only succeed under their usual conditions or such as are similar, and the desert plants would not grow in water or the water plants under desert conditions. The

life of an organism is thus only possible when its construction is in agreement with its environment, and it is ADAPTED TO THE CONDITIONS OF LIFE.

More penetrating morphological investigation soon shows that, while almost every member of the plant body has its functions, every peculiarity in construction cannot be regarded as adapted to these functions or to the environment. This can only be said of some of the characters of any part of the plant; for example, the abundance of the green pigment and the expanded form of foliage leaves stand in relation to the main functions of the leaf. Such characters are spoken of as useful to the organism. Many other characters are indifferent, such as, for example, the nature of the margin of leaves, described as entire, serrate, crenate, etc. Others may even be unfavourable so long as they are compatible with life, *e.g.* the absence of the green pigment from large portions of the leaf in many cultivated forms of Sycamore. Many adaptations appear to be less perfect than they could be. A character may be useful in one species while it is indifferent or even harmful in another. Such facts show clearly what care is requisite in judging of the significance of organic forms and structures; it is no easy matter to prove such assumptions by investigation (3).

2. There is a second direction in which morphology endeavours to attain a scientific understanding of the forms of plants. All existing plants are regarded as genetically related, the most highly organised with their diverse organs having gradually arisen phylogenetically from simple, unsegmented, unicellular forms. The organism and its parts have thus undergone manifold transformations in which, for example, particular organs by change of their structure took over new functions or became adapted to new conditions of life. It is thus a very important object of morphology to derive phylogenetically one form from another. Since the genetic development cannot be directly traced but has to be inferred, morphology is dependent on indirect methods in this problem. The most important indications are obtained by the study of the ontogeny of organisms and by the comparison of existing plants with one another and with those that lived in preceding ages. Within certain limits the ontogeny often repeats the phylogeny and thus contributes to the discovery of the latter. Comparative study connects divergent forms by means of intermediates. Since, however, the ontogeny never repeats the phylogeny completely or without alterations, and the connecting forms are often wanting, the results of morphology in this direction are correspondingly imperfect.

When the conviction has been reached after full investigation that diversely formed members of the plant body had a common phylogenetic origin, the hypothetical form from which we derive them is termed the PRIMITIVE FORM, and the changes undergone by it

in the course of descent its METAMORPHOSES. One of the most important results of morphology is the demonstration THAT THE VARIOUSLY FORMED PARTS OF EVEN THE MOST HIGHLY DIFFERENTIATED PLANTS ARE TO BE TRACED BACK TO A FEW PRIMITIVE FORMS. Those organs which have developed phylogenetically from a common primitive form are spoken of as HOMOLOGOUS, however different they may appear. The same morphological value is ascribed to them. For example, foliage leaves and the leaves of the flower (sepals, petals, stamens, and carpels) are homologous, and this extends to the leaf-tendrils (Fig. 209) and the leaf-thorns (Fig. 197). Organs of completely different structure and functions can thus be homologous. On the other hand, organs with similar construction and functions (*e.g.* tubers (Figs. 203, 205, 206), thorns (Figs. 197-199), tendrils (Figs. 208-210)) have often been genetically derived from different primitive forms. Such organs are spoken of as ANALOGOUS (for examples cf. p. 165 ff.).

Little differentiated structures with ill-defined functions, which we have reason to believe will in the future become transformed into more complete organs with well-marked functions, are termed RUDIMENTARY organs. Incomplete structures which have retrograded from more perfect ones are REDUCED organs.

3. Lastly, it is an aim of morphology to ascertain the causes or conditions which underlie the processes of external and internal differentiation of the plant and its parts, and of their inherited (phylogenetic) transformations. In this way it may be possible to ascertain clearly how in the course of descent adaptive characters have arisen. The study which concerns itself with such questions is EXPERIMENTAL MORPHOLOGY. Most of the problems of this are more conveniently dealt with as a section of physiology in relation to the other vital processes of the plant (developmental physiology or mechanics of development).

Morphology may be divided into external morphology and internal morphology or anatomy. Such a division would not, however, be suitable here, when it is desirable to regard the parts of the plant as organs with definite functions. For this it is necessary to show the intimate connection that frequently exists between the function of an organ and both its form and internal structure. From the outset we must be concerned with the plant as a living organism and not as a dead structure. The first question to be faced is with what life is most intimately connected, and this proves to be with a part only of the whole substance of the plant, namely, with the protoplasm. The protoplasm is, as a rule, enclosed in the cells which can be regarded as the elementary parts of the organism. The part of morphology which is concerned with the structure of cells is termed CYTOLOGY and will be dealt with first. The tissues formed by associated cells will then form the subject of a second part of morphology to which the name HISTOLOGY is given. Lastly, ORGANOGRAPHY deals with

the external members of the plant as its organs, taking into consideration both their external form and internal structure.

SECTION I

CYTOLOGY

THE CELLS AS THE BASIS OF LIFE

I. FORM AND SIZE OF CELLS

As already mentioned, both plants and animals are constructed of elementary parts known as cells. In the case of plants these are microscopically small chambers, the walls of which are formed of a firm membrane. In this respect they differ from animal cells. In the simplest cases the cells are spherical, but more commonly they have the form of small cubes, polyhedra, or prisms, which are associated in large numbers in the multicellular organs of plants. Elongated cells forming fibres or tubes are also of frequent occurrence.

FIG. 1.—Copy of a part of HOOKE's illustration of bottle-cork, which he described as "Schematism or texture of cork." Cf. Fig. 58.

These chambers, each of which consists of the cell wall or cell membrane enclosing the cavity or lumen of the cell, are as a rule so small as to be visible only when highly magnified. Their mean diameter is frequently between the hundredth and tenth of a millimetre. Owing to this it was long before the existence of cells was recognised. Occasionally cells attain a much greater size. Some sclerenchyma fibres adapted to special functions are 20 cm., while laticiferous tubes may be some metres in length.

The most important part of the cell is the protoplast or cell body occupying the cavity enclosed by the cell wall, since this is the living portion of the cell. On this account it is now natural to think rather of the living protoplast than of its enclosing chamber as the cell; a cell wall is completely wanting in the case of many "naked cells." In dead cells, it is true, the protoplasts have almost or completely disappeared, and such cells are only empty cell cavities. With the death of their protoplasts these cells need not lose their use to the plant. They are indeed essential in the construction of the more highly organised plants in which dead cells form the water-conducting tracts and contribute to mechanical rigidity.

It was due to the investigation of the cell walls that cells were recognised first in plants. An English micrographer, ROBERT HOOKE, was the first to notice

vegetable cells. He gave them this name in his *Micrographia* in the year 1667, because of their resemblance to the cells of a honeycomb, and published an illustration of a piece of bottle-cork having the appearance shown in the adjoining figure (Fig. 1). The Italian, MARCELLO MALPIGHI, and the Englishman, NEHEMIAH GREW, whose works appeared almost simultaneously in 1671, a few years after HOOKE'S *Micrographia*, were the true founders of vegetable histology. The living contents of the cell, the protoplast, was not recognised in its full significance until the middle of last century. Only then was attention turned more earnestly to the study of cytology, which, based on the works of SCHLEIDEN, HUGO V. MOHL, NÄGELI, FERDINAND COHN, and MAX SCHULTZE, was especially advanced by STRASBURGER.

II. THE LIVING CELL CONTENTS. THE PROTOPLAST (4)

A. The Constituent Parts of the Cell

If a thin longitudinal section of the growing point of the stem of one of the higher plants is examined under the high power of the microscope it is seen to consist of nearly rectangular cells (Fig. 2), which are full of protoplasm and separated from one another by delicate walls. If sections in various directions through the apex are compared, the conclusion is reached that the cells have the shape of small cubes or prisms.

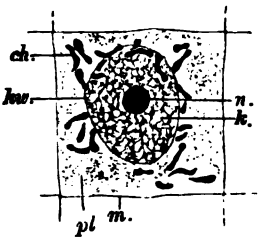


FIG. 2. Embryonic cell from the root-tip of the Oat. *k*, Nucleus; *kw*, nuclear membrane; *n*, nucleolus; *pl*, cytoplasm; *ch*, chromatophores; *m*, cell wall. (Somewhat diagrammatic. × about 1500. After LEWITZKY.)

In each of the cells a spherical or oval body, which fills a large part of the cell cavity, is distinguishable. This body (*k*) is the NUCLEUS of the cell. The finely granular substance (*pl*) filling in the space between the nucleus (*k*) and the cell wall (*m*) is the cell plasm, or CYTOPLASM. In the cytoplasm there are to be found around the nucleus a number of colourless and highly refractive bodies: these are the PLASTIDS or CHROMATOPHORES (*ch*). THE NUCLEUS, CYTOPLASM, AND CHROMATOPHORES ARE THE LIVING CONSTITUENTS OF THE CELL. They form together the protoplasm of the living cell body or PROTOPLAST. The nucleus and the chromatophores, which are always embedded in the cytoplasm, may be regarded as organs of the protoplast since they perform special functions. It is true that the particular functions of the nucleus are unknown, but it is certain that the interaction of nucleus and cytoplasm is necessary to maintain the life of the cell. In the lowest plants (Cyanophyceae and Bacteria) such a division of labour in the protoplasm is not certainly proved, the existence of the nucleus being still a matter of dispute (5). Chromatophores are wanting in the Bacteria and Fungi as in all animal cells.

In many animal cells an additional constituent of the protoplast has been demonstrated as a small body which is called a CENTRIOLE, in the immediate neighbourhood of the nucleus. Similar bodies are found in the vegetable kingdom in the cells of some Cryptogams, but are not of general occurrence even in them (Fig. 21 *A*).

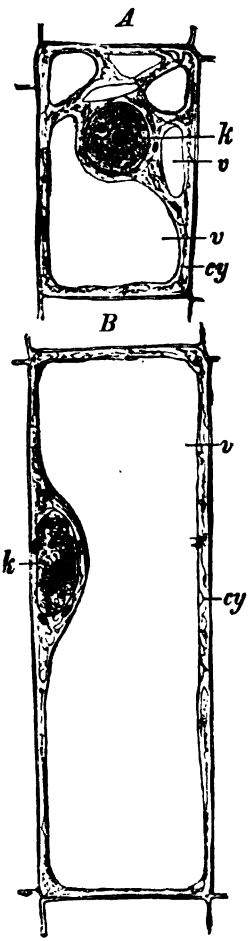


FIG. 3.—Two cells taken at different distances from the growing point of a phanerogamic shoot. *k*, Nucleus; *cy*, cytoplasm; *v*, vacuoles, represented in *B* by the sap cavity. (Somewhat diagrammatic. × circa 500. After STRASBURGER.)

It is only the embryonic cells of the plant, as they are met with in the apices of stem and root, which are thus completely filled with protoplasm. This does not hold for the fully developed cells of the plant which arise from these by growth in size and alterations of shape. During this transformation to cells of the permanent tissues the embryonic cells of plants, unlike those of animals, become poorer in protoplasm, since this does not increase in proportion to the growth of the cell. In every longitudinal section of the growing point of the stem it can be seen that at some distance from the tip the enlarged cells have already begun to show cavities or VACUOLES (*v* in *A*, Fig. 3) in their cytoplasm. These are filled with a watery fluid, the CELL SAP. The cells continue to increase in size, and usually soon attain a condition in which the whole central portion is filled by a single large sap cavity (*v* in *B*, Fig. 3). The cytoplasm then forms only a thin layer lining the cell wall, while the nucleus occupies a parietal position in the peripheral cytoplasmic layer (Fig. 3 *B*, *k*). At other times, however, the sap cavity of a fully-developed cell may be traversed by bands and threads of cytoplasm; and in that case the nucleus is suspended in the centre of the cell (Figs. 5, 10). But whatever position the nucleus may occupy, it is always embedded in cytoplasm; and there is always a continuous peripheral layer of cytoplasm lining the cell wall. This cytoplasmic peripheral layer is in contact with the cell wall at all points, and, so long as the cell remains living, it continues in that condition. In old cells, however, it frequently becomes so thin as to escape direct observation (Fig. 10), and is not perceptible until some reagent which attracts water and causes it to recede from the wall has been employed.

B. Main Vital Phenomena of Protoplasts

In order to facilitate an insight into the real character of protoplasm, attention will first be directed to the SLIME FUNGI (Myxomycetes), a group of organisms which stand on the border between the animal and vegetable kingdoms. The Myxomycetes are characterised at one stage of their development by the formation of a PLASMODIUM, a large, naked mass of protoplasm (Fig. 4). The cytoplasm consists of a clear ground substance, through which granules are distributed. This substance is of the consistence of a tenacious fluid; its superficial region is denser and free from granules, while these are numerous in the less dense central portion. The granules enable the internal streaming movements of the cytoplasm to be recognised. The currents are constantly changing their direction, moving either towards or away from the margin. The formation and withdrawal of processes of the margin stand in relation to the direction of the currents. When naked masses of protoplasm such as these plasmodia encounter foreign bodies, they can enclose them in vacuoles, and, when of use as food, digest them.

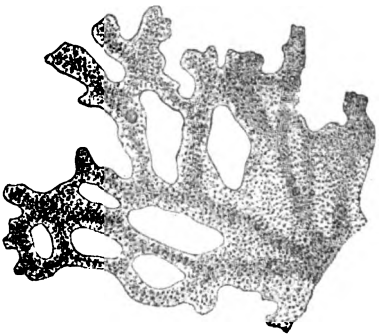


FIG. 4.—Portion of a full-grown plasmodium of *Chondrioderma difforme*. (× 90. After STRASBURGER.)

Even though bounded by a cell wall the cytoplasm frequently exhibits movements comparable to those of the naked amoebae and plasmodia of Myxomycetes. These movements are usually found in somewhat old cells. The stimulus caused by wounding the tissues in making the preparation frequently increases the activity of the movement (6); apparently it quickens the transport of nutrient material toward the wound. Such movements show that here also the protoplasm is of the nature of a tenacious fluid. When freed from the cell wall it assumes the form of a spherical drop. The cytoplasm, enclosed by a cell wall, may either exhibit isolated streaming movements, the direction of which may undergo reversals, or a single stream, the direction of which is constant. These two forms of movement are distinguished as CIRCULATION and ROTATION respectively. In rotation, which is found in cells with the cytoplasm reduced to a layer lining the wall, the single continuous current follows the cell wall. In circulation, on the other hand, the movement is found both in the layer lining the cell wall and in the strands traversing the vacuole. In no case does

the boundary layer of the protoplasm take part in the movement. Circulation is common in cells of land-plants, while rotation is more usual in water-plants.

When the protoplasm is in rotation, the cell nucleus and chromatophores are usually carried along by the current, but the chromatophores may remain in the boundary layer, and thus not undergo movement. This is the case with the Stoneworts (Characeae), whose long internodal cells, especially in the genus *Nitella*, afford good examples of well-marked rotation. A particularly favourable object for the study of protoplasm in circulation is afforded by the staminal hairs of *Tradescantia virginica*. In each cell (Fig. 5) currents of protoplasm flow in different directions in the peripheral cytoplasmic layer, as well as in the cytoplasmic threads, which traverse the sap cavity. These cytoplasmic threads gradually change their form and structure, and may thus alter the position of the cell nucleus.

FIG. 5.—Cell from a staminal hair of *Tradescantia virginica*, showing the nucleus suspended by protoplasmic strands. (× 240. After STRASBURGER.)

Movements in limited regions of protoplasts are seen in many of the lower Algae, especially in their swarm-spores. Near the anterior end of the swarm-spore the protoplasm may contain one or several minute pulsating vacuoles which appear and disappear rhythmically at short intervals. They empty suddenly, then reappear and slowly increase to their full size (Fig. 333, 1 *v*). The protoplast of the swarm-spore also possesses one or a number of threadlike contractile processes (cilia, flagella) which vibrate rapidly and serve as the motile organs of the cell.

Only within a narrow range of temperature is the protoplast actively alive, though life is preserved through a slightly more extended range. It dies and coagulates, as a rule, at temperatures slightly above 50° C. Alcohol, acids of suitable concentration, solution of mercuric chloride, etc., rapidly coagulate the protoplasm, and such substances are largely employed as fixing reagents in microscopical technique ([7]).

C. Chemical Properties of the Protoplast ([8])

Active protoplasm generally gives an alkaline, under certain conditions a neutral reaction, but never an acid one. It is not a simple substance chemically, but consists of a mixture of a large number of chemical compounds. Some of these undergo continual changes, upon which undoubtedly many important manifestations of the life of the protoplast depend. The most important components of the mixture are the proteids. The protoplasm thus shows the reactions of proteids, and when incinerated gives off fumes of ammonia. A whole series of proteids occur in the living protoplasm. In the nuclei proteids contain-

ing phosphorus (nucleo-proteids) predominate; these are not dissolved by pepsin, and only with difficulty by trypsin. Products of the dissociation of proteids, especially amides, are also contained in the protoplasm. Other components are enzymes, carbohydrates, and lipoids, such as fats and lecithin, in the condition of a fine emulsion; phytosterin (aromatic alcohols with the formula $C_{27}H_{45}OH$), and sometimes alkaloids and glucosides. The ash left after incineration shows that mineral substances are not wholly wanting in the protoplasm.

By the action of a dilute solution of potash, of chloral hydrate, or of eau de javelle, all parts of the protoplast are dissolved. Iodine stains it a brownish-yellow colour; acid nitrate of mercury (Millon's reagent), rose-red. Such reagents kill the protoplasm, after which their characteristic reactions are manifested. These reactions are given by proteid substances, but are not altogether confined to them.

D. Structure of the Parts of the Protoplast

Great assistance in the investigation of the structure of the protoplast is afforded by the processes of fixing and staining. Certain fixing agents harden and fix the protoplasm almost unaltered, but it is necessary to be on guard against the appearance of a structure in the process of coagulation ([9]).

The importance of staining depends upon the fact that the various constituents of the protoplast absorb dyes with different intensity and hold them more or less firmly when the preparation is washed. As a general rule only dead protoplasm is readily stained. For staining fixed vegetable protoplasts, solutions of carmine, haematoxylin, safranin, acid fuchsin, gentian violet, orange, methylene blue, etc., are employed.

1. The Cytoplasm.—This when highly magnified is seen to consist of a clear, hyaline, more or less tenacious fluid (HYALOPLASM) in which more or less numerous minute drops or granules (MICROSOMES) are embedded. The latter evidently are various products of the metabolism, and characterise the granular protoplasm or POLIOPLASM. The hyaloplasm itself is, however, not a simple solution. When investigated with the help of the ultra-microscope, an instrument which reveals granules and droplets too minute to be seen with the highest powers of the ordinary microscope, it is found to contain countless numbers of ultra-microscopic particles ([10]). This is a general characteristic of those solutions which the physical chemist recognises as COLLOIDAL SOLUTIONS or SOLS. The demonstration that protoplasm is a colloidal solution, and, in fact, an emulsion, is of fundamental importance. By its help many vital manifestations become susceptible of a physico-chemical explanation.

An extremely thin boundary layer free from granules is found at the periphery of the protoplast, and a similar layer bounds every vacuole present in the cytoplasm. The peripheral boundary layer and

the vacuole walls can be formed anew, but are nevertheless very important parts of the protoplast, since they determine the taking up of substances. They are semipermeable membranes, *i.e.* they allow water to pass, but are impermeable or only slightly permeable to many other substances.

Living protoplasm has frequently a foam-like structure. In dividing protoplasts fine filaments may appear which cease to be evident in the resting condition of the cell. It is not known whether the cytoplasm has a still finer internal structure which is not visible. When fixed and stained, a reticulate or honeycomb-like structure with embedded granules is formed as in other coagulated colloidal solutions.

In addition to the structures alluded to above, there have recently been demonstrated in the cytoplasm of both embryonic and permanent cells certain filamentous, spindle-shaped or dumb-bell-shaped structures. These are best seen after special fixation and staining, and agree so closely with the CHONDRIOSOMES (mitochondria) of embryonic animal cells that they have been given the same name ([11]). Probably they include bodies of various nature such as minute vacuoles, filamentous structures in the cytoplasm, young chromatophores, etc. They have been observed in some Mosses in the embryonic cells beside the chromatophores, and also in the Fungi.

FIG. 6.—Cell of the fungus, *Hypholoma fasciculare*, containing five nuclei. (× 500. After KNIEP.)

2. The Nucleus ([12]) has as a rule a spherical, oval, or lenticular form, but in long cells may be correspondingly elongated. In embryonic cells its diameter may amount to two-thirds of the total diameter of the protoplast. In full-grown cells of the permanent tissue, on the other hand, the nucleus is much less conspicuous, since it has not increased in size. Large nuclei are found in most Conifers, in some Monocotyledons, and in the Ranunculaceae and Loranthaceae among the Dicotyledons. Secretory cells are as a rule provided with especially large nuclei. On the other hand, the nuclei of the majority of Fungi (Fig. 6) and of many Siphoneae are very small.

While the cells of the Cormophytes are almost always uninucleate, in the Thallophytes, on the contrary, multinucleate cells are by no means infrequent. In many Fungi (Fig. 6), and in the Siphoneae among the Algae, they are the rule. The whole plant is then composed either of but one single multinucleate cell, which may be extensively branched and exhibit a complicated external form (Fig. 346), or it may consist of a large number of multinucleate cells, forming together one organism. Thus, on suitable treatment, several nuclei may be detected in the peripheral

cytoplasm of each of the cells of the common filamentous fresh-water Alga *Cladophora glomerata* (Fig. 7).

The living nucleus has a finely dotted appearance. It usually contains one or several larger, round, highly refractive granules or droplets, the use of which is unknown but which are called NUCLEOLI (Fig. 2 *n*). The nucleus, the consistence of which appears to be that of a tenacious fluid, is surrounded by a NUCLEAR MEMBRANE (Fig. 2 *kw*) by which the surrounding cytoplasm is separated from the NUCLEAR CAVITY.

Some insight into the finer structure of the nucleus is obtained from properly fixed and stained preparations. In these a deeply staining reticulum of CHROMATIN, which appears to consist mainly of proteids containing phosphorus, is evident. The nucleoli are situated in the meshes of the network within the nuclear cavity which is filled with the NUCLEAR SAP. The nucleoli stain deeply but differently from the chromatin.

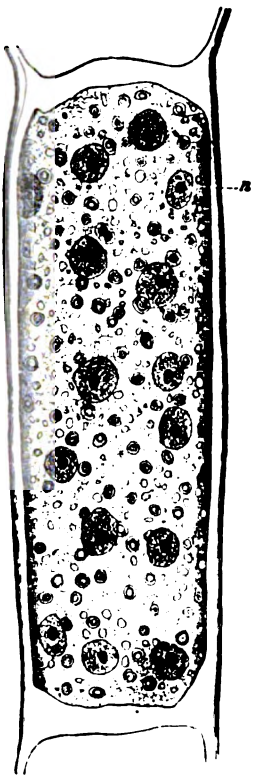


FIG. 7.—A cell of *Cladophora glomerata*, fixed with 1 per cent chromic acid and stained with carmine. *n*, Nuclei. (× 540. After STRASBURGER.)

In many nuclei the reticulum appears to be formed of a substance called LININ that stains feebly, and the chromatin to be embedded in this as minute granules. In some Algae and Fungi the nucleoli contain a proportion of the chromatin. They are thus not strictly equivalent to the nucleoli of the higher plants, as is further shown by their behaviour in the process of nuclear division (13).

It is still unknown what part the nucleus takes in the vital phenomena of the protoplast. It is, however, clear that it is necessary for the maintenance of life in nucleated cells. It also appears to be of great importance as the main bearer of the hereditary characters.

3. The Chromatophores (14). — In the embryonic cells of the embryo and of growing points, where the chromatophores (Fig. 2 *ch*) are principally located around the nucleus, they first appear as small, colourless, highly refractive bodies of circular, spindle-shaped or filamentous form. In older cells they attain a further development, as CHLOROPLASTS, LEUCOPLASTS, or CHROMOPLASTS. Since these bodies have the same origin they are all termed CHROMATOPHORES.

(a) Chloroplasts.—In parts of plants which are exposed to the light the chromatophores usually develop into chlorophyll bodies or chloroplasts. These are generally green granules of a somewhat flattened

ellipsoidal shape (Fig. 8), and are scattered, in numbers, in the parietal cytoplasm of the cells. All the chloroplasts in the Cormophytes, and for the most part also in the green Thallophytes, have this form. In the lower Algae, however, the chlorophyll bodies may assume a band-like (Fig. 328 *C*), stellate, or tabular shape. They are often reticulately perforated, *e.g. Cladophora* (Fig. 9). In these cases the chloroplast often includes one or more PYRENOIDS (Fig. 9 *py*); these are spherical protoplasmic bodies containing an albuminous crystalloid, and are surrounded by small grains of starch. No further structure can be distinguished in the living chlorophyll grains, which have a uniformly green colour. The green pigment,

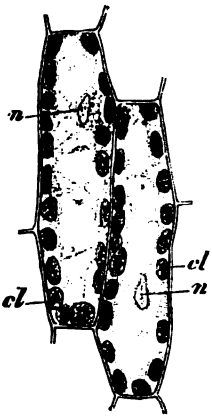


FIG. 8.—Two cells from a leaf of *Funaria hygrometrica*. *cl*, Chloroplasts; *n*, nucleus. (× 800. After SCHENCK.)

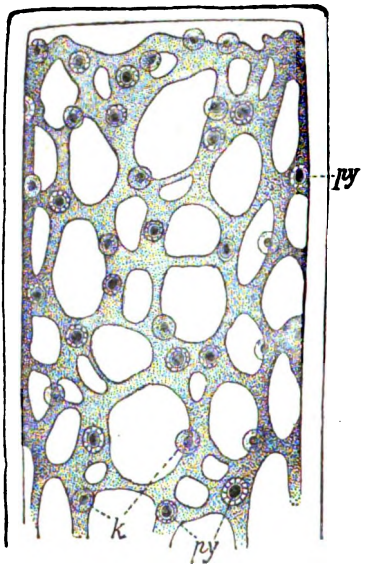


FIG. 9.—Reticulate chloroplast of *Cladophora arcta*. *py*, Pyrenoids; *k*, nuclei. (After SCHMITZ.)

chlorophyll, is essential for the decomposition of carbon dioxide in the chloroplasts.

The most recent investigations ([18]), especially those of WILLSTÄTTER and his pupils, have shown that four pigments are present in the chloroplasts. There are two closely related green pigments (chlorophyll *a* and *b*) in the proportions of 3 to 1, and two yellow pigments. The chlorophylls are esters of phytol, an alcohol of the formula $C_{20}H_{39}OH$, and a tri-carbon acid. They are thus compounds with large molecules containing carbon, oxygen, and hydrogen into the construction of which nitrogen and magnesium enter, but not, as was previously assumed, either phosphorus or iron. The blue-green CHLOROPHYLL *a* has the formula $C_{55}H_{72}O_5N_4Mg$, while that of the yellow-green CHLOROPHYLL *b* is $C_{55}H_{70}O_6N_4Mg$. The yellow pigments are the orange-red crystalline CAROTIN, hydrocarbons of the composition $C_{40}H_{56}$, one of which also occurs in the root of the carrot and the yellow crystalline

XANTHOPHYLL (oxide of carotin, $C_{40}H_{56}O_2$). Only the chlorophylls are concerned in the assimilation of carbon dioxide.

All four pigments can be extracted from the fresh or dried chloroplasts by various solvents, *e.g.* by acetone or 80-90 % alcohol. A deep-coloured solution containing all the pigments can be most readily obtained by pouring boiling alcohol on fresh leaves. Owing to the contained chlorophyll such a solution is deep green by transmitted light, but blood-red, owing to FLUORESCENCE, by reflected light. Its spectrum (Fig. 248) is characterised by four absorption bands in the less refractive portion and three in the more refractive half. The individual pigments can be separated by shaking the solution with various solvents. Thus benzol extracts the chlorophyll and accumulates as a green solution above the alcoholic solution which is now yellow. The amount of chlorophyll present in green parts of plants is relatively small, amounting, according to WILLSTÄTTER, to 0·5-1·0 % of the dry substance.

The variegated forms of some cultivated plants have larger or smaller areas of the leaf of a white or golden colour. The cells here contain colourless or yellow chromatophores instead of the green chloroplasts.

Many Algae are not green but exhibit other colours. In the blue-green, verdigris-green, blue, or less commonly violet-coloured Cyanophyceae, and in the red, violet, or reddish-brown chloroplasts of the Rhodophyceae, there are, in addition to the four pigments of the green chloroplasts, a blue pigment called PHYCOCYAN, and a red pigment, PHYCOERYTHRIN. These may occur singly or together, and both are readily dissolved from the dead cells by water containing a little alkali or neutral salt and yield a beautifully fluorescent solution. The phycocyan may often be found as a blue border surrounding one of the Cyanophyceae dried upon paper. Both pigments appear to be of proteid nature. Little is known as to their significance ([16]). In the Brown Algae the colour of the brown or yellow chloroplasts is due to their containing, in addition to chlorophyll *a* and a little chlorophyll *b*, carotin and xanthophyll, the reddish-brown FUCOXANTHIN ($C_{40}H_{54}O_6$), which is allied to the last-named pigment ([17]).

The colourings ([18]) which the leaves of trees assume in autumn before they fall are connected with a breaking down of the chloroplasts and their pigments. There remain in the protoplasts, in addition to a watery and often reddish-coloured fluid, only some oil-drops, crystals, and yellow highly refractive spheres. The case is different in those Coniferae whose leaves turn brown in winter and again become green in the spring; the changes undergone by the pigments in the chloroplasts are here reversible. The assumption of a brown colour by dying foliage-leaves is a *post mortem* phenomenon in which brown pigments soluble in water are produced.

In some phanerogamic parasites the chloroplasts are replaced by colourless, brownish, or reddish chromatophores, which may, however, in some of these plants still contain a trace of chlorophyll. In the Fungi chromatophores are completely wanting, as has already been mentioned.

(b) Leucoplasts.—In the interior of plants, where light cannot penetrate, leucoplasts are developed from the rudiments of the chromatophores instead of chloroplasts. They are usually of minute size (Figs. 5, 10 *l*), mostly spherical in shape, but often somewhat elongated in consequence of enclosed albuminous crystals (Fig. 28 *kr*). If the leucoplasts become exposed to the light, they may change into

chloroplasts. This frequently occurs, for example, in the superficial portions of potato tubers. The leucoplasts have, in many cells at least, the special function of transforming sugar into grains of starch, which appear within them.

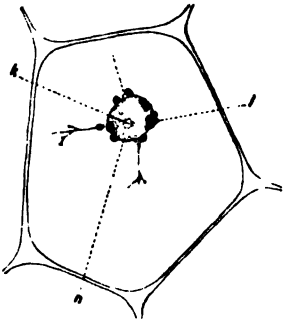


FIG. 10.—Cell from the epidermis of *Rhoeo discolor*. *n*, Nucleus with its nucleolus (*k*), and surrounded by the leucoplasts (*l*). Protoplasmic strands stretch from the nucleus to the layer of protoplasm, which is not represented, lining the wall. (× 240.)

(e) Chromoplasts. — These give the yellow and red colour to many parts of plants, especially to flowers and fruits. They arise from the colourless chromatophores of embryonic cells or from previously formed chloroplasts. They may resemble the chloroplasts in shape but are often smaller, while their colour is yellow or orange-red. This depends either on xanthophyll or carotin. The pigments are not uniformly dissolved in the chromoplast but form minute droplets (grana) in the plasmatic substance (the stroma) (19). The pigments, especially the carotin, readily crystallise out and the chromoplasts then become needle-shaped, triangular, or rhombic in form (Figs. 11, 12).

The origin and significance of the red EYE-SPOTS which are found in the cells of many Algae, especially in their motile cells, are insufficiently known. The eye-spot occurs in the neighbourhood of the chloroplast and is often connected with this (Fig. 333, 1 *a*). Some investigators hold that it

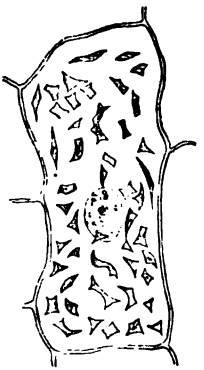


FIG. 11.—Cell from the upper surface of the calyx of *Tropaeolum majus*, showing chromoplasts. (× 540. After STRASBURGER.)

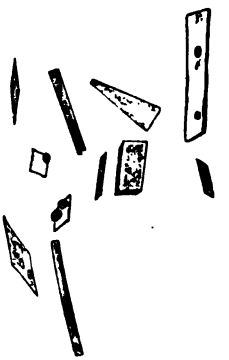


FIG. 12.—Chromoplasts of the Carrot, some with included starch grains. (× 540. After STRASBURGER.)

should be reckoned with the chloroplast and that it serves for the perception of light somewhat as the eye does. The red pigment, which has been termed HAEMATOCHROME, is simply carotin.

E. Origin of the Elements of the Protoplast (4)

All the living elements of the protoplast, the cytoplasm, the nucleus, and the chromatophores, are never newly formed but always arise from the corresponding elements of previous generations. They increase in mass by a process of growth, BUT THEY INCREASE IN NUMBER, LIKE THE PROTOPLAST AS A WHOLE, ONLY BY DIVISION OF THEIR KIND. In this way the properties of the living constituents of a germ cell are transmitted to all the cells of an organism and ultimately to its reproductive cells, the uninterrupted continuity of the life being maintained. The division of the protoplast is usually initiated by the division of the nucleus. In the case of uninucleate cells this intimate association of nuclear- and cell-division is necessary in order to ensure that each daughter cell has a nucleus. In the multinucleate cells (*e.g.* of Algae and Fungi) this is not essential, since each daughter protoplast would obtain the requisite nuclei, and as a matter of fact cell division in such cases is often independent of nuclear division.

It sometimes happens that the protoplast of a cell, without dividing, abandons its old cell wall. This process, which is called REJUVENATION of the cell, has nothing to do with cell division.

The rounding off of the protoplast in a cell of the green alga *Oedogonium*, and its emergence from an opening in the old cell wall as a naked swarm-spore, is an example of rejuvenation. Another is afforded by the protoplasts of the spores of mosses or ferns and of the pollen-grains of seed-plants surrounding themselves with a new cell wall within the old membrane, which then perishes.

1. Typical Division of the Protoplast. (a) Nuclear Division.—Except in a few cases, nuclei reproduce themselves by MITOTIC or INDIRECT DIVISION. This process, often referred to as KARYOKINESIS, is somewhat complicated.

Indirect Nuclear Division (20).—In its principal features the process is similar in the more highly organised plants and in animals. Its stages are represented in a somewhat diagrammatic manner in the following figure (Fig. 13) as they occur in a vegetative cell such as those which compose the growing point.

The fine network of the resting nucleus (Fig. 13, 1 *n*) becomes drawn together at definite points and separated into a number of bodies (Fig. 13, 2 *ch*), the outline of which is at first irregular. Their form soon becomes filamentous, and the filaments become denser and at the same time shorter and thicker (3, 4), and stain more deeply. The filaments are called CHROMOSOMES. Each chromosome undergoes a longitudinal split which continues to become more marked (5). The chromosomes, which become shorter, thicker, and smooth (6), are moved into the plane of division where they constitute the nuclear or equatorial plate (7 *kp*), a stellate figure (aster) which

usually lies in the future plane of division of the cell. It is seen in surface view in Fig. 14.

While the nuclear network is separating into the individual chromosomes, cytoplasmic filaments become applied to the nuclear membrane, surrounding it with a fibrous layer. This layer becomes raised up from the nuclear membrane at two opposite points (6 *k*) and forms the polar caps. The filaments converge at the poles,

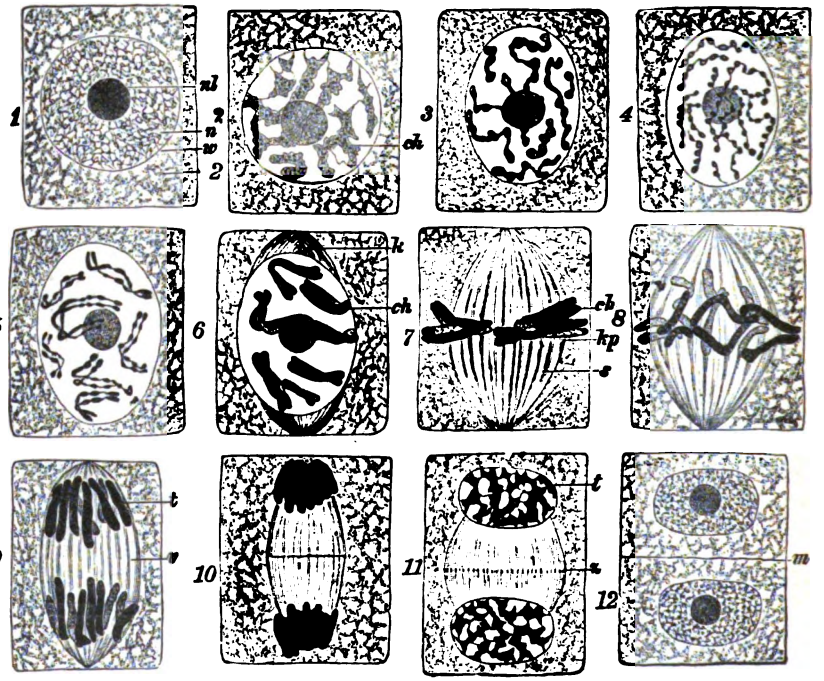


FIG. 13.—Successive stages of nuclear and cell division in a meristematic cell of a higher plant. Somewhat diagrammatic. Based on the root of *Najas marina*, fixed with the chrom-osmium-acetic mixture and stained with iron haematoxylin. *n*, Nucleus; *nl*, nucleolus; *w*, nuclear membrane; *ch*, chromosomes; *k*, polar caps; *s*, spindle; *kp*, nuclear plate; *t*, daughter nucleus; *v*, connecting fibres; *z*, cell-plate; *m*, new partition wall. The chromatophores are not visible with this fixation and staining. (× about 1000. After CLEMENS MÜLLER.)

where they constitute two pointed bundles. At this stage the nucleoli (*nl*) are dissolved and the nuclear membrane disappears. The fibres proceeding from the polar caps can thus become prolonged into the nuclear cavity (7). Here they either become attached to the chromosomes, or filaments from the two poles may come into contact and extend continuously from the one pole to the other. In this way the nuclear spindle (7 *s*) is formed. The two halves of each chromosome separated by the longitudinal split now separate in opposite directions

as the daughter chromosomes in order to form the daughter nuclei (10-12 *t*). During this stage (diaster) the chromosomes are as a rule U-shaped with the bends towards the poles of the spindle. Having reached the poles they crowd together, while the surrounding cytoplasm forms the nuclear membrane delimiting the new nuclei. Within the latter the chromosomes again assume a reticulate structure (11) and unite with one another to form a network (12), within which their individual limits are not distinguishable. We are compelled, however, to assume that the individuality of the chromosomes is not lost. The young nuclei enlarge and one or more nucleoli again appear within them (12).

The end attained by this mechanism of division is that the substance of the nucleus, and especially of the chromosomes, is distributed as equally as possible to the two daughter nuclei at each division. From this it may be concluded that the chromatin is especially important for the life of the cell and of the whole organism, and that the chromosomes play the main part in the transmission of hereditary qualities.

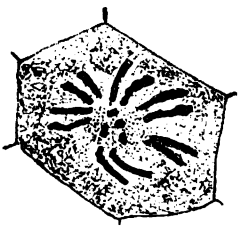


FIG. 14.—Young cells from a transverse section of the root-apex of *Galtonia candicans*, showing a nuclear plate in the polar view. The chromosomes are grouped in pairs. (× 1600. After STRASBURGER.)

The number of chromosomes occurring in any nucleus is a definite one, and when a deviation from the usual number is met with, it is due to some of the chromosomes having remained united end to end ([21]). The chromosomes of a nucleus may be of different sizes (Fig. 14); when such differences in size exist they persist in successive divisions. The smallest number of chromosomes which has yet been found in the nuclei of vegetative cells of the more highly organised plants has been six; as a rule the number is much larger.

In the lowest divisions of the vegetable kingdom, in some Algae and Fungi, the process of indirect nuclear division is simplified, the masses of chromatin being less carefully divided between the daughter nuclei ([13]).

The changes occurring in a mother nucleus preparatory to division are termed the PROPHASES of the karyokinesis. These changes extend to the formation of the nuclear plate, and include also the process of the longitudinal division of the chromosomes. The stage of the nuclear plate is the METAPHASE. The separation of the daughter chromosomes is accomplished in the ANAPHASE, and the formation of the daughter nuclei in the TELOPHASE of the division. The real purpose of the whole process is attained in the quantitative and qualitative division of the chromosomes, resulting from their longitudinal splitting. The anaphases and telophases of the karyokinesis are but a reverse repetition of the prophases. The reversal of the stages in the process of nuclear division commences with the separation of the daughter chromosomes. The stage of the nuclear plate at

which the progressive is replaced by the regressive movement tends to last a considerable time.

It is uncertain in what way the chromosomes are so precisely moved in the process of karyokinesis as described above. STRASBURGER assumed that the fibres of the spindle which appear to end at the chromosomes (traction fibres) by their shortening drew the daughter chromosomes from the nuclear plate to the poles, while the fibres extending from the one pole to the other were supporting fibres to the spindle. This assumption does not, however, explain the movement of the chromosomes toward the nuclear plate.

In certain reproductive cells of plants and animals resulting from fertilisation the nuclear division proceeds in a special manner and differs from the typical process just described. It is termed the reduction division, or meiosis (cf. p. 208).

Direct Nuclear Division ([22]).—In addition to the mitotic or indirect nuclear division there is also a DIRECT or AMITOTIC division, sometimes called FRAGMENTATION. Direct division of the nucleus occurs in nuclei which were themselves derived by indirect division. It is essentially a process of constriction which need not, however, result in new nuclei of equal size. Instructive examples of direct nuclear division are afforded by the long internodal cells of the Stoneworts (Characeae).

In the case of the Stoneworts, after a remarkable increase in the size of the nucleus, several successive rapid divisions take place, so that a continuous row of beadlike nuclei often results. While in uninucleate cells indirect nuclear division is followed by cell division, this is not the case after direct nuclear division.

(b) Multiplication of the Chromatophores.—This is accomplished by a direct division, as a result of which, by a process of constriction, a chromatophore becomes divided into nearly equal halves. The stages of this division may best be observed in the chloroplasts (Fig. 15).

FIG. 15.—Chlorophyll grains from the leaf of *Funaria hygrometrica*, resting, and in process of division. Small included starch grains are present in the grains. (× 540. After STRASBURGER.)

(c) Division of the Cytoplasm.—In the uninucleate cells of the higher plants cell division and nuclear division are, generally, closely associated. The fibres of the spindle extending from pole to pole persist as CONNECTING FIBRES between the developing daughter nuclei (Fig. 13, 9 *v*), and their number is increased by the interposition of others (Fig. 13, 10, 11). In consequence of this a barrel-shaped figure, the PHRAGMOPLAST is formed. At the same time the connecting fibres become thickened (Fig. 13, 11) at the equatorial plane, and the short rod-shaped thickenings form what is known as the CELL PLATE. In the case of cells rich in protoplasm or small in diameter the connecting fibres become more and more extended, and touch the cell wall at all points of the equatorial plane. The elements of the cell plate unite and form a cytoplasmic limiting layer, which then splits into two. In the plane of separation the new partition wall is formed of cell-wall

substance, and thus SIMULTANEOUSLY divides the mother cell into two daughter cells (Fig. 13, 12 *m*).

If, however, the mother cell has a large sap cavity, the connecting utricle cannot at once become so extended, and the partition wall is then formed SUCCESSIVELY (Fig. 16). In that case, the partition wall first commences to form at the point where the utricle is in contact with the side walls of the mother cell (Fig. 16 *A*). The protoplasm then detaches itself from the part of the new wall in contact with the wall of the mother cell, and moves gradually across until the septum is completed (Fig. 16 *B* and *C*); the new wall is thus built up by successive additions from the protoplasm.

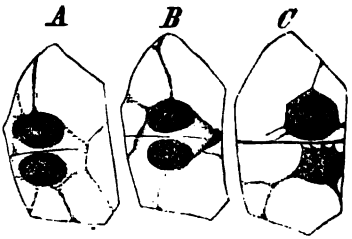


FIG. 16.—Three stages in the division of a living cell of *Epipactis palustris*. (× 865. After TREUB.)

In the Thallophytes, even in the case of uninucleate cells, the partition wall is not formed within connecting fibres, but arises either simultaneously from a previously formed cytoplasmic plate, or successively, by gradual projection inwards from the wall of the mother cell. In this form of cell division the new wall commences as a ring-like projection from the inside of the wall of the mother cell, and gradually pushing farther into the cell finally extends completely across it (Figs. 17, 18). In a division of this sort, in

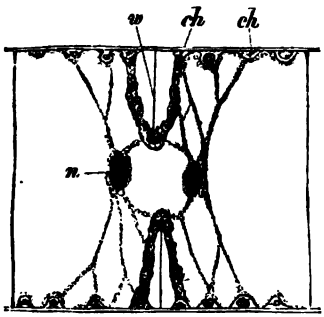


FIG. 17.—Cell of *Spirogyra* in division. *n*, One of the daughter nuclei; *w*, developing partition wall; *ch*, chloroplast pushed inward by the newly forming wall. (× 280. After STRASBURGER.)

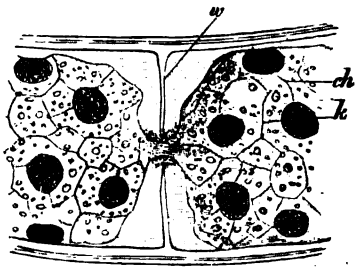


FIG. 18.—Portion of a dividing cell of *Cladophora fracta*. *w*, Newly forming partition wall; *ch*, dividing chromatophore; *k*, nuclei. (× 600. After STRASBURGER.)

uninucleate cells, nuclear division precedes cell division, and the new wall is formed midway between the daughter nuclei (Fig. 17).

In multinucleate cells a cell division does not follow on each nuclear division. Among Algae and Fungi there are large and externally segmented forms which consist internally of a single

protoplasmic mass with many nuclei; this is not divided into chambers by cell walls.

2. Deviations from typical Cell Division.—The main deviations from typical cell division which are found here and there in the vegetable kingdom are MULTICELLULAR FORMATION, CELL-BUDDING, and FREE CELL FORMATION.

(a) Free Nuclear Division and Multicellular Formation.—The nuclear division in the multinucleate cells of the Thallophytes may serve as an example of free nuclear division, that is, of nuclear division unaccompanied by cell division. In plants with typical uninucleate cells, examples of free nuclear division also occur. This method of development is especially instructive in the embryo-sac of Phanerogams, a cell, often of remarkable size and rapid growth, in which the future embryo is developed. The nucleus of the rapidly growing embryo-sac divides, the two daughter nuclei again divide, their successors repeat the process, and so on, until at last thousands of nuclei are often formed. No cell division accompanies these repeated nuclear divisions, but the nuclei lie scattered throughout the peripheral cytoplasmic lining of the embryo-sac. When the embryo-sac ceases to enlarge, the nuclei surround themselves with connecting strands, which then radiate from them in all directions (Fig. 19). Cell plates make their appearance in these connecting strands, and from them cell walls arise. In this manner the peripheral protoplasm of the embryo-sac divides simultaneously into as many cells as there are nuclei. All intermediate stages between simultaneous multicellular formation and successive cell division can be found in embryo-sacs. Where the embryo-sac is small and of slow growth, successive cell division takes place, so that multicellular formation may be regarded as but a shortened process of successive cell division, induced by an extremely rapid increase in the size of the cell.

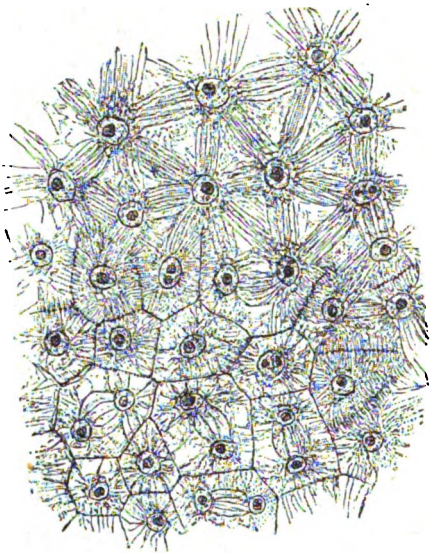


FIG. 19.—Portion of the peripheral protoplasm of the embryo-sac of *Reseda odorata*, showing the commencement of multicellular formation. This progresses from above downwards. From a fixed and stained preparation. (× 240. After STRASBURGER.)

(b) Cell-budding.—This is simply a special variety of ordinary cell division, in which the cell is not divided in the middle, but, instead, pushes out a protuberance which, by constriction, becomes separated from the mother cell. This mode of cell multiplication is characteristic of the Yeast plant (Fig. 20); the spores, known as conidia and basidiospores, which are produced by numerous Fungi, have a similar origin (Fig. 398).

(c) Free Cell Formation.—Cells produced by this process differ conspicuously

from those formed by the usual mode of cell division, in that the free nuclear division is followed by the formation of cells, which have no contact with each other, and in the formation of which the whole of the cytoplasm of the mother cell is not used up. This process can be seen in the development of the swarm cells of some Algae, in the developing embryo of the Gymnosperms, in *Ephedra*, for example, and also in the formation of the spores of the Ascomycetes. A single nucleus is present

FIG. 20.—*Saccharomyces cerevisiae*. *1*, Cells without buds; *2* and *3*, budding cells. (× 540. After STRASBURGER.)

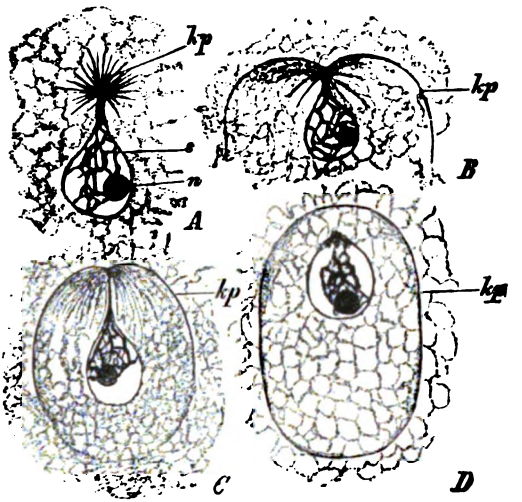


FIG. 21.—Successive stages of the delimitation of a spore in the ascus of *Erysiphe communis*. *s*, Nuclear network; *n*, nucleolus. (× 1500. After HARPER.)

to begin with in each ascus of the Ascomycetes. By successive divisions eight nuclei lying free in the cytoplasm are derived from this. A definite portion of cytoplasm around each of these nuclei becomes limited by a peripheral layer, which then forms a cell wall. Thus eight separate spores arise (cf. Fig. 381). As the researches of Harper ([22]) have shown, the formation of the peripheral layer proceeds from a centrosome-like mass of kinoplasm (Fig. 21 *A*) which formed a pole of the spindle in the preceding nuclear division. The nucleus is drawn out towards this mass of kinoplasm. From the latter kinoplasmic radiations proceed (*kp*) which surround the spore as it becomes delimited, and finally fuse to form its peripheral layer (Fig. 21 *B*, *C*, *D*).

III. THE LARGER NON-LIVING INCLUSIONS OF THE PROTOPLASTS ([24])

In addition to the minute microsomes which are always present in the cytoplasm, larger non-living inclusions make their appearance in the cytoplasm and chromatophores of all cells as they pass from the meristematic to the mature condition. The cell sap, which in larger or smaller vacuoles is hardly ever absent from a cell of the mature tissues of a plant, has already been mentioned. Besides these droplets of a watery solution, fats and oils and also solid bodies in the amorphous or crystalline condition frequently occur in the cell sap or the cytoplasm itself. Many of these included substances

are of great value in the life of the plant as RESERVE MATERIALS. They are accumulated in considerable quantity for future use in the cells of storage organs (bulbs, tubers, seeds). Others are end products of metabolism which may, however, be of great ecological importance.

A. Inclusions of the Cytoplasm

1. Fluid Inclusions of the Cytoplasm. (a) The Cell Sap.—This name is given to the watery fluid in the larger vacuoles or the single sap cavity of vegetable cells (Fig. 3). It is more or less rich in various dissolved substances, which are sometimes reserve materials and at others end products of metabolism; solid inclusions, especially in the form of crystals, also occur in it. The substances in the cell sap may be the same or different from those in the protoplasm. The dissolved substances may differ in the various vacuoles of the same cell.

All cell sap contains in the first place INORGANIC SALTS, especially nitrates, sulphates, and phosphates. Its reaction is usually acid owing to the presence of ORGANIC ACIDS (*e.g.* malic acid, which is constantly present in the leaves of succulent plants, tartaric acid, oxalic acid, etc.), or salts of these.

The SOLUBLE CARBOHYDRATES are especially important constituents of the cell sap, often as reserve materials. Various SUGARS (cane-sugar, maltose or malt-sugar, glucose or grape-sugar) are the most important. Cane-sugar is frequently stored as a reserve material, as in the sugar-beet, carrot, the stem of the sugar-cane, and other plants from which sugar is obtained. A similar place is taken by the carbohydrate INULIN in the Compositae and by GLYCOGEN in the Fungi. Carbohydrates are transported throughout the plant in the form of sugar.

If preparations containing glucose be placed in a solution of copper sulphate, and, after being thoroughly washed, are transferred to a solution of caustic potash and heated to boiling, they will give a brick-red precipitate of cuprous oxide. If cane-sugar or saccharose be present, this treatment gives only a blue colour to the cell sap. Treated with alcohol, inulin is precipitated in the form of small granules, which may be redissolved in hot water. When portions of plants containing much inulin, such as the root tubers of *Dahlia variabilis*, are placed in alcohol or dilute glycerine, the inulin crystallises out and forms sphaerites, spheroidal bodies composed of radiating crystal needles; these sphere-crystals often show distinct stratification and are easily broken up into wedge-shaped portions.

GLYCOGEN, which is of frequent occurrence in animal tissues, occurs in the Fungi, Myxomycetes, and the Cyanophyceae in the form of droplets. In the Fungi it takes the place of other carbohydrates such as starch and sugar. Cytoplasm containing glycogen is coloured reddish-brown with a solution of iodine. This colour almost wholly disappears if the preparation be warmed, but reappears on cooling.

MUCILAGE is often found in the cells of bulbs, as in *Allium cepa* and *Urginea* (*Scilla*) *maritima*; in the tubers of Orchids; also in aerial organs (Fig. 22), especially

in the leaves of succulents, and also outside the protoplasts in the cell wall (cf. p. 38).

AMIDES, especially Asparagin and also ALBUMINOUS SUBSTANCES, occur in the cell sap as reserve materials or as intermediate products of the metabolism (cf. p. 14 for reactions).

Highly refractive vacuoles filled with a concentrated solution of TANNIN [25] are of frequent occurrence in the cytoplasm of cortical cells, and may often grow to a considerable size. ALKALOIDS, GLUCOSIDES, and BITTER PRINCIPLES allied to these are also not infrequent in the cell sap. All these are usually end products of metabolism.

The dark-blue or green colour reaction obtained on treatment with a solution of ferric chloride or ferric sulphate, and the reddish-brown precipitate formed with an aqueous solution of potassium bichromate, are usually accepted as tests for the recognition of tannin, although equally applicable for a whole group of similar substances. The tannins are not further utilised in the plant. They often impregnate cell walls, which then persist and resist decay.

The cell sap is often coloured, principally by the so-called ANTHOCYANINS, a group of non-nitrogenous glucosides. They are blue in an alkaline, and red in an acid-reacting cell sap, and, under certain conditions, also dark-red, violet, dark-blue, and even blackish-blue. Alkalies frequently change the colour to green. Anthocyanin can be obtained from the cell sap of a number of deeply coloured parts of plants in a crystalline or amorphous form. Less commonly yellow substances, ANTHOCLORE and ANTHOXANTHINE, are found dissolved in the cell sap as in the yellow floral leaves of the Primrose and the yellow Foxglove. A brown pigment called ANTHOPHAEINE occurs in the cells of the blackish-brown spots of some flowers.

The researches of WILLSTÄTTER and his pupils [26] have advanced our knowledge of the chemical constitution of the anthocyanins. They are glucosides in which cyanidins (aromatic pigment components, hydroxyl compounds of phenylbenzopyrilium, and apparently related to the flavones), are combined with sugar, *e.g.* in the Cornflower cyanidin ($C_{15}H_{10}O_6$) and in the flower of the Larkspur delphinidin ($C_{15}H_{10}O_7$). In red flowers the cyanes are united with acids and in blue flowers with alkalies, while the pigments in violet flowers are neutral. The anthoxanthins also are glucosides with aromatic pigment components which belong to the flavones.

Blood-coloured leaves, such as those of the Copper Beech, owe their characteristic appearance to the united presence of green chlorophyll and anthocyanin. The autumnal colouring of leaves also depends on the formation of anthocyanin. The different colours of flowers and fruits which often serve to attract animals are due to the varying colour of the cell sap, to the different distribution of the cells containing the coloured cell sap, and also to the different combinations of dissolved colouring matter with the yellow, orange, or red chromoplasts and the green chloroplasts.

(b) Vacuoles containing Fats (Fatty Oils).—These substances are of common occurrence as reserve materials; about nine-tenths of all Phanerogams store them in their seeds. In seeds especially rich in oil this forms highly refractive droplets distributed through the cytoplasm (*e.g.* castor-oil in seeds of *Ricinus*) and may form 70 % of the dry weight. Fats are glycerine esters of fatty acids, especially of palmitic acid ($C_{16}H_{32}O_2$), stearic acid ($C_{18}H_{36}O_2$), and oleic acid ($C_{18}H_{34}O_2$). Since fats provide a greater amount of energy than other storage substances, the space available is best utilised for them.

(c) Vacuoles with Ethereal Oils and Resins [27].—These also occur as highly refractive droplets. They are found in the cells of many petals. Special cells, often with corky walls and filled with resin or ethereal oils, are found in the rhizomes of certain plants, as for instance in those of *Acorus Calamus* and of Ginger (*Zingiber officinale*); also in the bark, as, for example, of Cinnamon trees (*Cinnamomum*); in the leaves, as in the Sweet Bay (*Laurus nobilis*); in the pericarp and seed of the Pepper (*Piper nigrum*); in the pericarp of Anise (*Illicium anisatum*). Ethereal oils and resins have antiseptic properties. In flowers their scent assists in attracting insects. Under some conditions the oil assumes the crystalline form, *e.g.* in rose petals.

2. Solid Inclusions of the Cytoplasm. (a) Crystals of Calcium Oxalate.—Few plants are devoid of such crystals. They are formed in the cytoplasm as end products of metabolism, within vacuoles which afterwards enlarge and sometimes almost fill the whole cell. In such cases the other components of the cell become greatly reduced; the cell walls at the same time often become corky, and the whole cell becomes merely a repository for the crystal. The crystals may be developed singly in a cell, in which case they are of considerable size (Fig. 130 *k*, 175 *Bk*, 184 *k*), or many minute crystals may fill the cell as a crystalline sand. In other cases they form crystal aggregates (Fig. 130 *k*, 186 *k*), clusters of crystals radiating in all directions from a common centre, or many needle-shaped crystals lie parallel forming a bundle of raphides (Fig. 22). The various types of crystals predominate in different plants.

The LARGE SOLITARY CRYSTALS belong to the tetragonal or to the monosymmetric system, the concentration of the mother-liquor from which they crystallise out determining which system is followed. The stellate CRYSTAL AGGREGATES radiating from an organic nucleus are particularly common. In Monocotyledons and in many Dicotyledons RAPHIDES are of widespread occurrence (Fig. 22), the bundle of crystals being always enclosed in a large vacuole filled with mucilage.

SILICEOUS BODIES, which are only soluble in hydrofluoric acid, are found in the cytoplasm of many cells, especially of Palms and Orchids, and often completely fill the whole cell.

(b) Aleurone Grains. Proteid Crystals.—Albuminous substances may be stored in a dissolved form in the cell sap of succulent parts of plants. Thus they can be precipitated by treatment with alcohol in the cells of the potato tuber. In dry structures, such as many seeds,

proteid substances occur as solid granules called ALEURONE GRAINS, which are especially large in oily seeds (Fig. 23). They are formed from vacuoles, the contents of which are rich in albumen, and harden into round grains or, sometimes, into irregularly shaped bodies. The albuminous substances of which they consist are mainly globulins (28). A portion of the albumen often crystallises, so that frequently one and occasionally several crystals are formed within the aleurone grain. In aleurone grains containing albumen

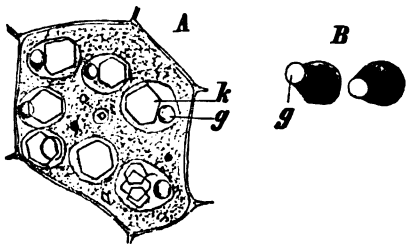


FIG. 23.—*A*, Cell from the endosperm of *Ricinus communis*, in water; *B*, isolated aleurone grains in olive oil; *k*, albumen crystals; *g*, globoid. (× 540. After STRASBURGER.)

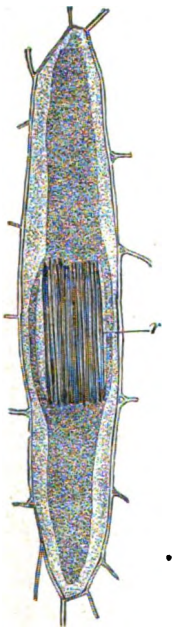


FIG. 22.—Cell from the cortex of *Dracæna rubra*, filled with mucilaginous matter and containing a bundle of raphides, *r*. (× 160. After SCHENCK.)

FIG. 24.—Part of a section of a grain of wheat, *Triticum vulgare*. *p*, Pericarp; *t*, seed coat, internal to which is the endosperm; *al*, aleurone grains; *am*, starch grains; *n*, cell nucleus. (× 240. After STRASBURGER.)

crystals there may often be found globular bodies termed GLOBOIDS (Fig. 23 *g*), which consist of globulins combined with the calcium and magnesium salt (phytin) of an organic phosphoric acid (phytic acid). Crystals of calcium oxalate are also found enclosed in aleurone grains. Free globoids are found in the cytoplasm of some seeds. In the cereals the aleurone grains, which lie only in the outer cell layer of the seeds (Fig. 24 *al*), are small, and free from all inclusions; they contain neither crystals nor globoids. As the outer cells of wheat

grains contain only aleurone, and the inner almost exclusively starch, it follows that flour is the richer or poorer in albumen, the more or less completely this outer layer has been removed before the wheat is ground. The aleurone layer remains attached to the inner layer of the seed-coat, in the bran.

Reactions for aleurone are the same as those already mentioned for the albuminous substance of protoplasm. Treatment of a cross-section of a grain of wheat (Fig. 24) with a solution of iodine would give the aleurone layer a yellow-brown colour.

ALBUMEN CRYSTALS.—Crystals of albumen are of relatively frequent occurrence in vegetable tissues and are often found in aleurone grains (Fig. 23); especially large crystals are found in the endosperm of the Brazil nut (*Bertholletia excelsa*). Albumen crystals may also occur directly in the cytoplasm; as, for instance, in the cells poor in starch, in the peripheral layers of potatoes, and in chromatophores (Fig. 28). Albumen crystals are sometimes found even in the cell nucleus. This is particularly the case in the Toothwort (*Lathraea*), and in many Scrophulariaceae and Oleaceae. Albumen crystals usually belong either to the regular or to the hexagonal crystal system. They differ from other crystals in that, like dead albuminous substances, they may be stained, and also in that they are capable of swelling by imbibition.

B. Inclusions of the Chromatophores

Crystals of albumen and of pigments have already been mentioned as occurring in chromatophores (Fig. 28), but the most important inclusion is STARCH ([29]). The chloroplasts in plants exposed to the light almost always contain starch grains (Fig. 15). These grains of starch found in the chloroplasts are formed in large numbers, but as they are continually dissolving, always remain small. Large starch grains are found only in the reservoirs of reserve material, where starch is formed from the deposited products of previous assimilation. Such starch is termed RESERVE STARCH, in contrast to the ASSIMILATION STARCH formed in the chloroplasts. It also only arises in chromatophores, in this case the LEUCOPLASTS or starch-builders which form it from sugar.

All starch used for economic purposes is reserve starch. The amount of starch contained in reservoirs of reserve material is often considerable; in the case of potatoes 20 per cent of their whole weight is reserve starch, and in wheat the proportion of starch is as high as 70 per cent. The starch flour of economic use is derived by washing out the starch from such reservoirs of reserve starch. In the preparation of ordinary flour, on the contrary, the tissues containing the starch are retained in the process of milling.

The reserve starch consists of flat or roundish (oval or circular) grains, differing in size in different plants. A comparison of the accompanying figures (Figs. 25-27), all equally magnified, will give

an idea of the varying size of the starch grains of different plants. The size of starch grains varies, in fact, from 0·002 mm. to 0·170

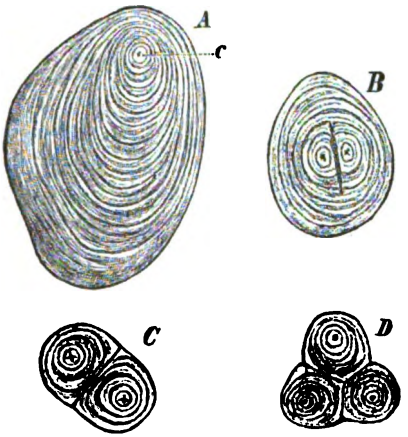


FIG. 25.—Starch grains from a potato. *A*, simple; *B*, half-compound; *C* and *D*, compound starch grains; *c*, organic centre of the starch grains. (× 540. After STRASBURGER.)

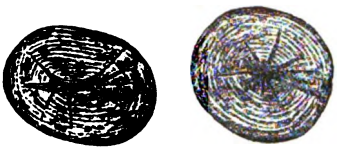


FIG. 26.—Starch grains from the cotyledons of *Phaseolus vulgaris*. (× 540. After STRASBURGER.)

FIG. 27.—Starch grains of the oat, *Avena sativa*. *A*, Compound grain; *B*, isolated component grains of a compound grain. (× 540. After STRASBURGER.)

mm. Starch grains 0·170 mm. large may be seen even with the naked eye, as minute bright bodies. The starch grains stored as reserve material in potatoes are comparatively large, attaining an average size of 0·09 mm. As shown in the above figure (Fig. 25 *A*), they are plainly stratified. The stratification is due to the varying densities of the successive layers; thicker denser layers which appear clear by transmitted light alternate with thinner less dense layers which appear dark. They are excentric in structure, since the organic centre, about which the different layers are laid down, does not correspond with the centre of the grain but is nearer to one margin. The starch grains of the leguminous plants and cereals, on the other hand, are concentric, and the nucleus of their formation is in the centre of the grain. The starch grains of the kidney bean, *Phaseolus vulgaris* (Fig. 26), have the shape of flattened spheres or ellipsoids; they show a distinct stratification, and are crossed by fissures radiating from the centre. The disc-shaped starch grains of wheat are of

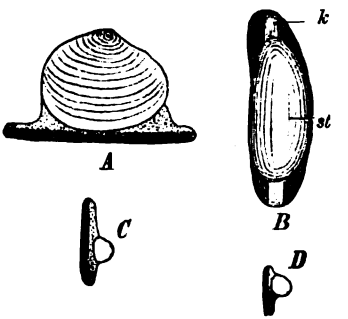


FIG. 28.—Leucoplasts from an aerial tuber of *Phajus grandifolius*. *A*, *C*, *D*, viewed from the side; *B*, viewed from above; *st*, starch grain; *kr*, proteid crystal. (× 540. After STRASBURGER.)

two very different sizes, and only indistinctly stratified. In addition to the simple starch grains so far described, half-compound and compound starch grains are often found. Grains of the former kind are made up of two or more individual grains, surrounded by a zone of peripheral layers enveloping them in common. The compound grains consist merely of an aggregate of individual grains unprovided with any common enveloping layers. Both half-compound (Fig. 25 *B*) and compound starch grains (Fig. 25 *C*, *D*) occur in potatoes, together with simple grains. In oats (Fig. 27) and rice all the starch grains are compound. The compound starch grains of rice consist of from 4 to 100 single grains; those of the oat of about 300, and those of *Spinacia glabra* sometimes of over 30,000. Starch grains have thus distinctive forms in different plants.

The structure of starch grains becomes intelligible in the light of their mode of formation. If the starch grain is uniformly surrounded by the leucoplast during its formation, it grows uniformly on all sides and is symmetrical about its centre. If the formation of a starch grain begins near the periphery of a leucoplast, the grain will grow more rapidly on the side on which the main mass of the leucoplast is present, and the starch grain thus becomes excentric (Fig. 28). Should, however, several starch grains commence to form at the same time in one leucoplast, they become crowded together and form a compound starch grain, which, if additional starchy layers are laid down, gives rise to a half-compound grain.

Starch grains are composed of a carbohydrate with the formula $(C_6H_{10}O_5)_n$. When it is to be employed further in the metabolism of the plant, starch is again transformed into sugar by the action of an enzyme called DIASTASE.

Starch grains may be regarded as crystalline structures, sphaero-crystals, or sphaerites, which are built up of radially arranged, needle-shaped crystals of α- and β-amylose. With polarised light they show, like inorganic sphaerites, a dark cross, an appearance depending on the doubly-refractive nature of the elements of the starch grain. The stratification may be the expression of differences in form and abundance of the crystalline needles in the successive layers.

Starch grains are as a rule coloured, first blue and then almost black, by a watery solution of iodine; the grains of glutinous rice, however, stain wine-red, possibly consisting of amylodextrine. They are easily swollen at ordinary temperatures in solutions of potash or soda and by chloral hydrate. They also swell and form a paste in water at 70°-80° C. They dissolve, *i.e.* are transformed into sugar without previous swelling, in concentrated sulphuric acid. Heated without the addition of water, or roasted, the starch is transformed into an imperfectly known substance that is soluble in water.

IV. THE CELL WALL (30)

Each protoplast in plants is as a rule enclosed by a firm investment called the cell wall. This is formed on the outside of the

protoplast and is not itself regarded as living. Many plants commence their development as naked protoplasts, *e.g.* swarm-spores or egg-cells. These cells, before developing further and dividing, secrete a thin cell wall clothing the surface. In cell division, as has already been described, a partition wall is usually formed between the new cells so that each protoplast remains enclosed by a cell wall.

The form of cells is usually dependent on the cell wall, for the naked protoplast behaves like a fluid drop. The relatively small and uniformly shaped meristematic cells attain their ultimate size and special shapes by the **growth in surface** of their walls. This growth is sometimes the same all round, and at other times is limited to the tip or an angle of the cell, to a girdle-like zone, or some other circumscribed region. It comes

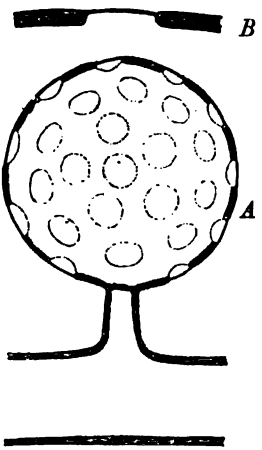


FIG. 29.—*A*, Spherical stalked cell of *Saprolegnia* with circular pits in the wall. *B*, One pit of this in optical section more highly magnified.

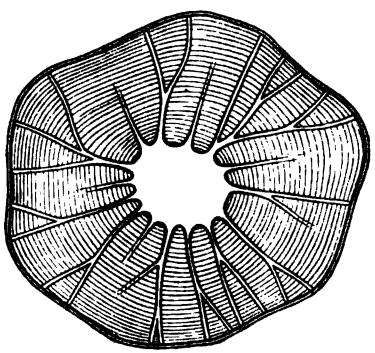


FIG. 30.—Sclerotic cell from the shell of a walnut showing stratification of the wall and branched pits. The canals of some of these pass obliquely out of the plane of section. (ROTHERT, adapted from REINKE.)

about as a result of the stretching and sometimes the rupture of the wall and the secretion and deposit of new cell-wall substance by the protoplast (GROWTH BY APPOSITION), or else by the insertion of new material between the particles of the existing wall (GROWTH BY INTUSSUSCEPTION).

The cell wall serves to protect and also to give rigidity to the protoplast. This is attained both by the tension of the membrane (TURGOR, cf. p. 225) and by the **growth in thickness** of the cell wall. The thin and structureless walls become as a rule thickened either uniformly or so that parts remain relatively thin, while others grow in thickness. In many cells the whole extent of the wall is thickened with the exception of small circular, elliptical, or spindle-shaped areas which form the PITS. These appear in the thickened wall as

depressions (Fig. 29) or tubular canals (Fig. 30), closed at one end, as a rule the outer, by the unthickened portion of the cell wall which forms the pit membrane (Fig. 29 *B*). Sometimes with the increase in the thickness of the wall the canals of several pits unite forming BRANCHED PITS. Such branched pits have usually very narrow canals and occur for the most part in extremely thick and hard cell walls as, for instance, those of sclerotic cells or sclereides (Fig. 30). In other cells the greater part of the wall is only slightly thickened, while narrowly circumscribed portions thicken greatly and assume the form of projections, warts, simple or branched pegs (Fig. 31), spines (Fig. 32), ridges, bands or a network (Figs. 67, 68). Such thickenings may form either on the outside (centrifugal) or on the inner surface of the wall (centripetal). Small projections often occur on hairs, while the thickenings of spores and pollen grains (Fig. 32) and in many water-conducting cells of the higher plants (Figs. 67, 68) are characteristic.

FIG. 31.—Portion of a tubular rhizoid of *Marchantia* with local peg-like thickenings of the wall.

A very peculiar form of thickening with calcium carbonate deposited in it and localised to one small region of the wall is seen in the CYSTOLITH which forms a stalked body, hanging in the cell like a bunch of grapes (*Ficus elastica*, Fig. 33).

The growth in thickness, which commences during the growth in surface of the wall, continues after this is complete. It is usually effected by apposition, *i.e.* the deposition of material by the protoplasm on the already existing wall in the form of new layers or lamellae. In this way a concentric stratification of the cell wall arises (Fig. 30). In the thickened wall thicker, denser lamellae alternate with thinner and less dense layers, which are often not only richer in water but chemically different from the denser layers. The latter are more highly refractive and appear brighter. In many, apparently homogeneous, cell walls such stratification can be recognised after swelling has been brought about by treatment with strong acids or alkalies.

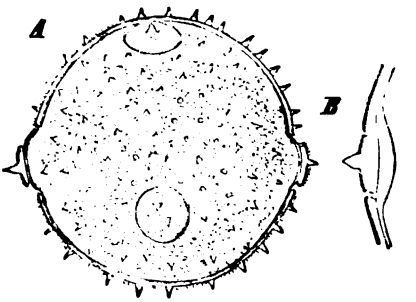


FIG. 32.—*A*, Pollen-grain of *Cucurbita Pepo* in surface view, and partly in optical section, rendered transparent by treating with oil of lemons. (× 240.) *B*, Part of transverse section of pollen grain of *Cucurbita verrucosa*. (× 540. After STRASBURGER.)

Not uncommonly growth in thickness also depends on the introduction of new material into the existing wall (intussusception).

Centrifugal thickening of the wall is frequently brought about by intussusception. This can take place at some distance from the protoplasm and be associated with

chemical and structural differentiation of the cell wall, which thus behaves almost as if it were a living structure. The centrifugal thickening of the walls of cells which have arisen by free cell formation (*e.g.* ascospores) is effected by the periplasm from which the cells have been cut out (cf. p. 27). Similarly the thickenings of many pollen grains and spores are deposited from without by the protoplasm of the tapetal cells which line the cavities in which they are developed. The protoplasts of the tapetum fuse to a periplasmodium surrounding the young spores or pollen grains [31].

In some cases fine striae, running obliquely to the longitudinal axis of the cell, are apparent when the thickening layers are viewed from the surface (Fig. 34). This striation depends either on a distinction in the individual thickening layers of regions of different density, the denser frequently projecting into the cell cavity, or (in many Algae such as *Cladophora*) on a wave-like folding of the lamellae. If the wall is distinctly stratified the striae in successive thickening layers are usually inclined in opposite directions (Fig. 34).

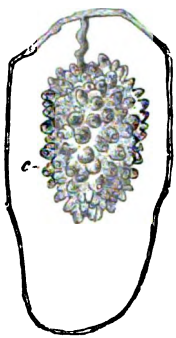


FIG. 33.—Cell of *Ficus elastica* containing a cystolith, *c*. (× 240. After SCHENCK.)

FIG. 34.—Part of a sclerenchymatous fibre from *Vinca major*. The striations of the outer layers are more apparent than those of the inner layers. The thickness of the wall, as seen in optical section, is also shown. (× 500. After STRASBURGER.)

Chemical Nature of the Cell Wall [32].—Although capable of the above processes of growth the cell wall is from the outset not a living portion of the protoplast but a product secreted by the latter. In course of time it can undergo changes of a chemical nature. In living cells it is always permeated by water and swollen, but shrinks correspondingly when the water is more or less completely removed. The lamellae of the wall consist of CARBOHYDRATES, in the main of CELLULOSES, but also of HEMICELLULOSES or PENTOSANES, and as a rule of several of these substances. The cell walls thus never consist of pure cellulose. The celluloses occur in the walls of all plants with the exception of most fungi; they are polysaccharides, the composition of which is expressed by the formula $(C_6H_{10}O_5)_n$. They stain blue with chlor-zinc-iodide solution but not with iodine alone. This

reaction holds for many hemicelluloses which are also polysaccharides. The cell wall nearly always contains other substances in considerable amount, some of which are stained other colours than blue by chlor-zinc-iodide. The PECTIC SUBSTANCES are especially important; these take a yellow colour with this reagent. It depends on this that many "cellulose walls" do not give a pure blue with chlor-zinc-iodide but stain violet, brownish violet, or brown. CHITIN is present in the walls of most Fungi and Bacteria. This substance, formerly regarded as peculiar to the animal body, replaces cellulose in the case of the Fungi ([33]).

The celluloses are insoluble in dilute acids and alkalies; even concentrated potash solution does not dissolve them. They are, on the other hand, soluble in ammonia-oxide of copper, by concentrated sulphuric acid after conversion into dextrose, and by a special enzyme (cytase) formed by plants. After treatment with sulphuric or phosphoric acid a watery solution of iodine will colour them blue, and a similar reaction is obtained by the simultaneous action of a concentrated solution of certain salts, such as zinc-chloride or aluminium-chloride, and of iodine. Accordingly chlor-zinc-iodide, on account of the blue or violet colour imparted by it, is one of the most convenient tests for cellulose. The name of hemicelluloses is given to a series of substances which are nearly related to the celluloses, but are transformed by even dilute acids into soluble sugars other than dextrose. They are often insoluble in ammonia-oxide of copper. As the celluloses are polysaccharides with large molecules produced from hexoses ($C_6H_{12}O_6$), the pentosanes ($C_5H_8O_4)_n$ are corresponding condensation products of pentoses ($C_5H_{10}O_5$) such as arabinose and xylose. The pectins are characterised by the ease with which they dissolve in alkalies after previous treatment with dilute acids. In contrast to cellulose, they stain deeply with safranin and methylene blue. The pectins are complex compounds in which monohexoses, pentosane, and in addition methyl alcohol behaving as an ester and calcium and magnesium behaving as salts, are united to tetragalacturic acid ($C_{24}H_{34}O_{25}$, a condensation product of galacturic acid $C_6H_{10}O_7$) ([34]).

Chitin is a polysaccharide containing nitrogen; it contains acetyl-acetic-acid in an acid-amide-like combination.

The cell wall frequently undergoes chemical changes of various kinds during the life of the cell; sometimes layers already deposited change, in other cases the newly deposited layers are different from those first formed. These transformations stand in the closest relation to the requirements of the plant to which the cells contribute. As regards "cellulose walls," these in young cells are less elastic but relatively more extensible than in older cells; this is advantageous in relation to the active growth in length of young parts. Such walls offer little resistance to the diffusion of water and dissolved substances.

Cellulose walls not infrequently become MUCILAGINOUS, their substance being transformed into a gelatinous or mucilaginous mass which swells greatly in water. Frequently cell walls undergo LIGNIFICATION, SUBERISATION, or CUTINISATION. Lignification diminishes the extensibility of the cells considerably, and increases their rigidity

without lessening the permeability of the wall to water and dissolved substances. Corky and cutinised walls, on the other hand, are relatively impermeable to water and gases, and greatly diminish evaporation. The cell walls are frequently coloured dark by derivatives of tannins, and thus, as in seed-coats and in the old wood, are protected against decay. In old cell walls inorganic substances often accumulate in considerable amount. Silicic acid is frequent, calcium carbonate less common, while organic salts such as calcium oxalate also occur.

LIGNIFICATION depends on the introduction into the carbohydrate layers of the cell wall of various substances which are mainly benzole derivatives. The innermost layers of the wall of lignified cells consist, however, in many cases of cellulose. Characteristic reactions for lignin are a yellow colour with acid aniline sulphate, and a red colour with phloroglucin and hydrochloric acid. With chlor-zinc-iodide lignified walls stain yellow, not blue. KLASON ([32]) regards these reactions as dependent on a condensation product of coniferyl- and oxyconiferyl-alcohol which he calls lignin.

SUBERISATION is as a rule limited to the middle thickening layers of a cell wall. The corky lamellae consist of SUBERIN only and thus contain no carbohydrate. CUTINISATION is closely related to suberisation but not identical. It consists in a secondary deposit of CUTIN on a cellulose wall, or its introduction into the substance of the wall. No sharp distinction can be drawn between cutin and suberin. Both are coloured brownish yellow by chlor-zinc-iodide and take a nearly identical yellow colour with potash; they stain red with sudan-glycerine and are both insoluble in concentrated sulphuric acid or ammonia-oxide of copper. Cutin, however, resists the action of potash better. Both cutin and suberin behave differently to reagents according to their special mode of origin. According to VAN WISSELINGH ([33]) suberin is a fatty substance which is composed of glycerine esters and other compound esters of phellonic, suberic, and others of the higher fatty acids; the phellonic acid, which is a constant constituent of suberin, is wanting in cutin.

CALCIUM CARBONATE occurs in the walls of certain plants, *e.g.* of most Characeae, in such amount that they become rigid and brittle. SILICIC ACID is present in the peripheral cell walls of grasses, horse-tails, and many other plants (*e.g.* of the unicellular diatoms), and makes them more rigid. CALCIUM OXALATE when present is usually in the form of crystals.

The pigments belonging to the flavone group which occur in the technically valuable woods are also localised in the cell walls.

Solid cell walls may undergo a transformation into GUM, as in the gummosis of wood. In species of *Prunus* and *Citrus* the thickening layers of the cell wall become swollen one after another in this process, and ultimately the cell contents are involved in the change ([36]).

SECTION II

HISTOLOGY ([37])

THE CELLS AS ELEMENTARY UNITS OF THE BODY

I. THE FORMATION OF TISSUES

A. The Idea and Significance of Cellular Tissues

Every close association of protoplasts enclosed in cell walls is termed a tissue.

Only the lowest organisms are composed of a single uninucleate or multinucleate protoplast and are thus unicellular throughout their life. Usually the body of a plant is multicellular, consisting of many protoplasts separated by cell walls and thus forming a tissue. The attainment of large size and more complex external organisation is as a rule associated with such a structure. There are, it is true, certain Algae (Siphoneae) which are externally highly organised, while they consist internally of a single multinucleate protoplast. These may be contrasted as non-cellular organisms with the ordinary cellular plant, to the construction of which they form an exception. The formation of a cellular tissue is of the greatest importance in the development of more highly organised plants in enabling a division of labour to be effected in the protoplasm of the body. The division of the protoplasm into numerous protoplasts provides elementary parts which can take over different duties. The cell walls separating the protoplasts isolate the latter more or less, while at the same time increasing the cohesion and the internal rigidity of the whole body formed of the numerous soft protoplasts.

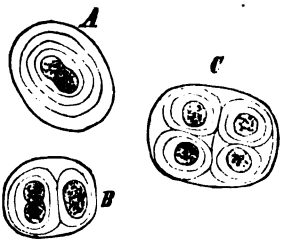


FIG. 35.—*Gloeocapsa polydermatica*. *A*, Commencement of division; *B*, (to the left) shortly after division; *C*, a resting stage. (× 540. After STRASBURGER.)

A very imperfect tissue formation is found in those organisms the cells of which separate from one another at each division, but remain connected by the mucilage derived from the swollen cell walls. Such unions of more or less independent cells that have had a common origin may be termed cell families or cell colonies. The Schizophyceae, to which group *Glococapsa* (Fig. 35) belongs, and the orders of the Volvocales and Protococcales among the Green Algae afford numerous examples, and the descriptions in the special part should be consulted.

In the cell filaments and cell surfaces of those lower Algae in which the cells are all equivalent but are united together, the characters of a definite tissue begin to make their appearance. With the increasing number of cells composing the organism we get a contrast between base and apex and the appearance of a growing point, and also progressive division of labour among the cells.

B. Origin of Tissues

A continuous aggregation of cells in intimate union is called a tissue. The origin of vegetable tissues is, in general, attributable to cell division. In *Hydrodictyon* among the Algae a tissue is formed by the apposition of free cells. In the Fungi and Siphoneae a tissue arises through the interweaving of tubular cells or cell filaments (Fig. 37). In such cases, where the filaments are so closely interwoven as to form a compact mass of cells, the tissue thus formed has the same appearance as the tissues of higher plants (Fig. 36). The mutual interdependence of the cells of a tissue is manifested both by the conjunction of their pits and by the general similarity of their wall thickenings.

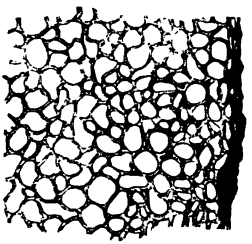


FIG. 36.—Transverse section of the sclerotium of *Claviceps purpurea*. (× 300. After SCHENCK.)

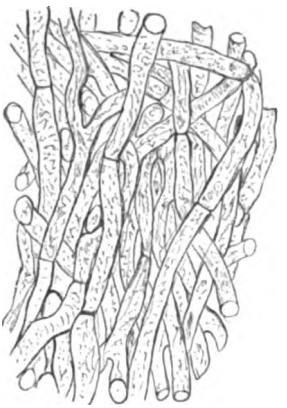


FIG. 37.—Longitudinal section of the stalk of the fructification of *Boletus edulis*. (× 300. After SCHENCK.)

C. The Cell Walls in the Tissues

When sections of vegetable tissues are examined under a low magnification the attention is attracted mainly or only by the cell walls. These appear to form a network of threads something like a woven tissue, and the name takes its origin from this inaccurate comparison.

The cell walls exhibit peculiarities resulting from the connection of the cells and characteristic of particular tissues.

1. Stratification.—All the septa arising in the course of cell divisions in tissues are at first very thin and simple lamellae, common to the two cells the protoplasts of which they separate. The cell wall never remains in this condition. Even in meristematic cells it becomes thickened as the membrane grows in surface extent. Thickening only ceases long after the cell has reached its ultimate size. It varies according to the functions taken over by the cell as part of a permanent tissue, especially thick walls being found in cells which contribute to the mechanical rigidity of the plant (Fig. 38). As a

rule the thickening of a partition wall is effected by the two adjoining protoplasts depositing new lamellae on both sides of the original thin septum (Figs. 38, 40, 62). The thickening may thus be equal or unequal on the two sides and each protoplast comes to have its own surrounding layers. The common middle region of the wall is called the middle lamella (Fig. 38 *m*). It is as a rule very thin, only widening out somewhat at the angles where several walls meet (Fig. 71 *Cm**), and consists mainly of pectic substances containing calcium; it is relatively easily dissolved. In lignified and suberised tissues the middle lamella is also lignified.

In soft tissues even boiling in water may swell the middle lamella and so separate the cells (*e.g.* many kinds of potatoes). In ripe fruits this separation

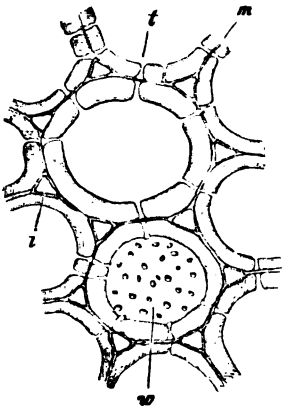


FIG. 38.—Strongly thickened cell from the pith of *Clematis vitalba*. *m*, Middle lamella; *i*, intercellular space; *t*, pit; *w*, pitted cell wall in surface view. (× 300. After SCHENCK.)

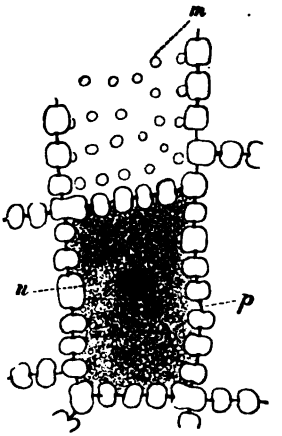


FIG. 39.—Cells from the endosperm of *Ornithogalum umbellatum*. *m*, Pits in surface view; *p*, closing membrane; *n*, nucleus. (× 240. After STRASBURGER.)

occurs naturally. Treatment with Schulze's macerating fluid (potassium chlorate and nitric acid) or with concentrated solution of ammonia will separate other cells by destroying the middle lamella. The macerating fluid will thus isolate the elements of wood. There are also certain Bacteria which ferment pectic substances and thus bring about the separation of the cells; in this way the mechanical cells of Flax are isolated in the process of retting.

The thickening layers are distinguishable from the middle lamella both by their optical and chemical properties. Since they usually lie equally on both sides of the middle lamella the whole wall acquires a more or less symmetrical construction (Figs. 38-40, 41, 62) which extends to the pitting. Three distinct layers can frequently be distinguished in strongly thickened cell walls, such as those of the wood, a primary, a secondary, and a tertiary thickening layer; these

differ in their optical appearance and their chemical composition. The secondary thickening layer is usually the most strongly developed, and forms the chief part of the cell wall. The tertiary or innermost layer is usually more highly refractive (Fig. 71 *Ci*); it consists as a rule of cellulose.

Cell walls which do not adjoin other cells (Figs. 40, 44) and especially the external walls of the plant are, on the other hand, asymmetrically constructed. In such cases thickening layers can only be deposited on the side of the original cell wall which faces the cavity of the cell.

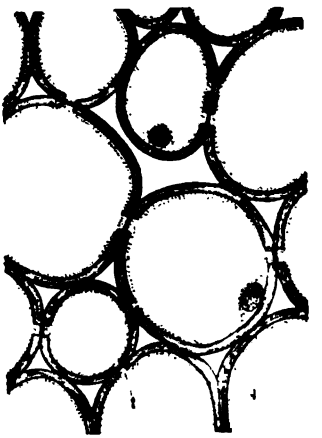


FIG. 40.—Cells from the cortex of *Iris florentina*. *t*, Pits in the stratified cell wall; *i*, intercellular spaces. (× about 400.)

2. Pitting.—The cell walls which separate the protoplasts will evidently render difficult the passage of materials from cell to cell in proportion to the thickness of the wall. The life of the organism could not continue without such transport of material. It is therefore necessary that this should not be too greatly hindered by the thickening of the walls that ensures rigidity. The difficulty is met by the formation of pits in the walls between the protoplasts, while pits are as a rule wanting in the free external walls.

The pits, which in greatly thickened walls form canals with circular (Figs. 38 *w*, 39 *m*) or elliptical cross section, meet accurately, and would form one continuous canal were it not that the unthickened primary wall persists as a pit membrane (Figs. 38 *t*, 39 *p*, 40 *t*). The openings of narrow elliptical pits into adjoining cells usually appear to cross one another obliquely.

The structure of pits may be very easily seen in the greatly thickened and abundantly pitted cell walls of the seeds of various Palms, Liliaceae, and other Monocotyledons (*Ornithogalum*, Fig. 39). The thickening here consists of a hemicellulose which forms a reserve material in the seed, and at germination is dissolved by an enzyme. The walls have a gleaming, white appearance, and are so hard that such seeds, *e.g.* of the Palm, *Phytelephas macrocarpa*, are technically known and employed as vegetable ivory.

3. Connections of the Protoplasts in Tissues.—The harmonious co-operation of all the living parts of the body, which is such a striking feature of the life of an organism as a whole, would hardly be possible if the protoplasts forming the tissues were completely divided from one another by the cell walls. It can in fact be shown that the protoplasts of the plant are united together by extremely find

cytoplasmic filaments, which proceed from the boundary layer of the cytoplasm and are known as plasmodesms (38). Such filaments are mostly confined to the pit membrane (Fig. 41 *s*), but may also penetrate the whole thickness of the cell wall (Fig. 42 *pl*). The existence of these connecting filaments of living substance between the protoplasts confers an organic unity on the whole body of the plant, serving for the conduction both of substances and of stimuli.

4. Cell Fusions.—Rapid transport of substances within the body of the multicellular plant is necessary, for instance from one organ to another, as from the leaves to the roots. The process of diffusion through the cell walls or the movement of substances in the very fine plasmodesms

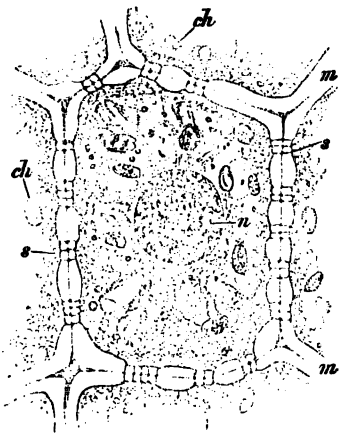


FIG. 41.—A cell from the cortex of the Mistletoe (*Viscum album*); the protoplast has been properly fixed and stained and the wall (*m*) swollen. The pit membranes (*s*) are traversed by connecting threads; *ch*, chloroplasts; *n*, nucleus. (× 1000. After STRASBURGER.)

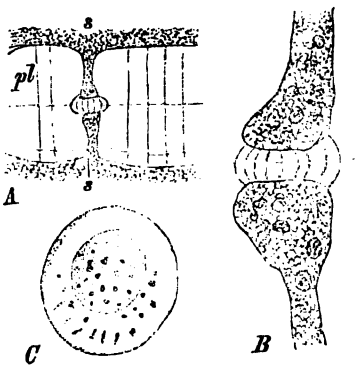


FIG. 42.—*A*, A swollen portion of cell wall from the endosperm of the Vegetable Ivory Palm (*Phytelephas macrocarpa*). At *s*, *s*, simple pits filled with cytoplasm; in the intervening pit membrane are fine connecting threads (plasmodesms); *pl*, other threads traversing the whole thickness of the wall. (× 875.) *B*, The contents of two opposed pits and the connecting threads of the pit membrane. (× 1500.) *C*, the opening of a pit and the connecting threads of the pit membrane viewed from the surface. The smaller circle indicates the canal of the pit, while the larger circle is the pit membrane; the dark points on the latter are the plasmodesms. (× 1500. After STRASBURGER.)

does not suffice to meet this need, even when assisted by the presence of the pits, which have been seen to correspond in the walls separating adjoining cells. The cavities of many cells, especially those which serve for transport, therefore become continuous by relatively wide openings, so that they form tubular structures or CELL FUSIONS. Such openings arise singly or in numbers by a solution of the cell-wall substance, especially in the end walls of adjoining cells.

5. Formation of Intercellular Spaces and the Ventilation of the Tissues.—Usually as the meristematic cells are transformed into permanent tissue and the cell walls thicken, the middle lamella splits

locally, especially at the angles of the cells. At these points the walls of neighbouring cells separate and INTERCELLULAR SPACES filled with air arise throughout the plant (Figs. 38, 40 *i*). In accordance with their mode of origin the smaller intercellular spaces are triangular or quadrangular in transverse sections. They form a connected system of narrow, branched canals (INTERCELLULAR SYSTEM) which traverse the tissues in all directions. From their mode of origin by the splitting of cell walls such intercellular spaces are termed SCHIZOGENOUS. Unequal growth of the tissues may lead to the complete isolation of cells or the formation of larger chambers or passages of more or less regular form. Intercellular spaces can also arise by the dissolution or breaking down of cells and are then termed LYSIGENOUS. Sometimes spaces, that are in their origin schizogenous, are further enlarged lysigenously. Whole regions of the tissue may be stretched and broken down by unequal growth. Hollow stems arise in this fashion. In tissues which have arisen by a weaving together of filaments (Fig. 37) the intercellular spaces are present from the outset.

Intercellular spaces usually contain air and are of great importance for the living cells forming the tissues. A single cell in water or air can obtain at any time the gases, especially oxygen, which are essential to its life from the surrounding medium. The life of the numerous protoplasts in the tissues of a plant requires a supply of oxygen. This introduction and circulation of gases in the tissues is carried out by the system of intercellular spaces.

II. KINDS OF CELLS, TISSUES, AND TISSUE-SYSTEMS

Only in the lower multicellular plants does the tissue consist of equivalent, spherical, polyhedral, and cylindrical cells (cf. *e.g.* Fig. 84), which are similarly able to perform all the vital functions. This tissue may be termed parenchyma. As the division of labour between the protoplasts increases, with increase in size and progressive external organisation, cells or groups of cells acquire diversity in form, structure, and function. There results in the higher plants a segregation of the originally uniform cells into variously constructed kinds of cells, connected, it is true, by intermediate forms. Comparative study of the various organs of a plant, or of the higher plants, shows that the number of these KINDS OF CELL is limited, and that DEFINITE FORMS OF CELLS RECUR IN THEM ALL.

Similar cells are usually associated in groups which constitute a KIND OF TISSUE. These are distinguished by the form, contents, and the walls of their constituent cellular elements, and each kind of tissue has its special function or functions. More highly organised plants are composed of a number of kinds of tissue, but, as in the case of kinds of cells, this number is small, since they recur in the most diverse plants. It is not uncommon for single cells (idioblasts)

or cell groups of a different structure and content to be found in an otherwise uniform type of tissue.

In the higher plants particular kinds of tissue may occur in considerable amount and extend in unbroken connection for a distance or through the whole plant body. These may often include several associated kinds of tissue and constitute MORPHOLOGICAL TISSUE SYSTEMS. Such compound associations of tissues may be characterised structurally and have different main functions. The functions of the different kinds of tissue within them tend to complement one another.

In a PHYSIOLOGICAL TISSUE SYSTEM are grouped together all cells that agree in their main functions, irrespectively of their morphological connection, or of their ontogenetic origin. Such physiological systems are thus something quite different from morphological tissue systems.

The tissue systems of the more highly organised plants can be divided into two main groups: (1) the meristematic or formative tissues; (2) the mature or permanent tissues.

A. The Formative Tissues

These are also termed MERISTEMS and consist either of relatively small cubical or isodiametric cells, or of prismatic, flattened, or elongated cells with thin walls, abundant protoplasm, large nuclei, and few and small vacuoles (cf. Fig. 2). The numerous cell divisions that occur in their cells is characteristic. These formative tissues, from which the permanent tissues are developed, are distinguished according to the place and mode of their origin into PRIMARY and SECONDARY MERISTEMS.

1. **Primary Meristems.** — These arise by the division of the germ cell and at first compose the whole embryo. Later they become localised at the growing points of the branches and roots (Figs. 102, 157), where the increase in number of meristematic cells and the formation of the rudiments of many lateral organs takes place (apical growth).

One or a number of the cells at the extreme tip of the growing point always remain meristematic, and multiply by growth and continued cell division following on this. The meristematic cells thus produced, after undergoing further divisions, become gradually transformed into cells of the permanent tissue. When there is a single cell at the tip distinguished by its form and size from the other meristematic cells it is called an APICAL CELL (Figs. 100, 101, 156); when there are a number of cells in one or more layers they are spoken of as INITIAL CELLS (Figs. 102, 157). The latter may resemble apical cells, but are often more like the other meristematic cells.

A short distance behind the growing point the similar cells of the primary meristem begin to grow differently and give rise to strands

and layers of variously shaped formative cells, which at first retain the general characters of meristematic cells (Figs. 100, 102, 157). Intercellular spaces, absent in the meristem itself, now arise. At a somewhat greater distance from the growing point the characters of the various permanent tissues make their appearance and become more marked basipetally until the mature structure is attained. In this process of tissue-differentiation groups, strands, or layers of cells may retain the meristematic characters and serve as places of origin later for a renewed formation of meristematic and mature tissues. Their power of division may persist throughout the life of the plant.

In many Monocotyledons the basal region of the internodes remains for a long time meristematic, and serves, in addition to the growing point, as a place of production of permanent tissue. In this way the intercalary growth of these and other plants is brought about.

2. Secondary Meristems are derived either from the above-mentioned inactive remains of the primary meristem or are newly formed from cells of the permanent tissue, which alter their function and by new cell divisions are transformed into meristematic cells. Their elements resemble those of the primary meristems, but as a rule have the form of elongated or flattened prisms. Such secondary meristems, which get the name CAMBIUM, give origin to cork and to the secondary growth in thickness of woody plants. They form a thin layer of prismatic meristematic cells (Figs. 169, 185) parallel to the surface of the organ at the outside of the cylinder of wood. In the cambium a middle layer of initial cells undergoes continued tangential divisions which cut off daughter cells to both the inside and outside in the radial direction. These cells after some further divisions are transformed into cells of the permanent tissues.

The new cell walls arising in the cell divisions of a meristem are flat and as a rule, though not without exception, placed at right angles to the pre-existing older walls. Walls more or less parallel to the surface of the organ are termed PERICLINAL, and those at right angles to this ANTICLINAL.

B. The Permanent Tissues

The cells of the permanent tissues differ from the meristematic cells in being as a rule larger, with relatively little protoplasm and large vacuoles, and sometimes completely dead. Cell divisions are not usually taking place in them, and the cell walls are variously thickened and often chemically altered. The permanent tissue is composed of a variety of kinds of cells and tissues with diverse functions. It is usually provided with intercellular spaces.

In developing from the meristem the cells of the permanent tissue enlarge, separate at places from one another, undergo thickening and chemical alterations of their walls, modify or lose their cell contents, and sometimes fuse by dissolution of the partition walls. In enlarging

or elongating the cells may behave independently (Fig. 174), so that the ends of some which elongate greatly push past, or in between, other cells (SLIDING GROWTH) (39).

The permanent tissues may be classified in various ways. Thus according to their origin primary and secondary permanent tissues may be distinguished arising from the corresponding meristems.

A morphologically useful division of the permanent tissues is obtained when all the differences of the component cells are taken into consideration together.

It was formerly usual to take the dimensions of the cells into special consideration, and on this ground PARENCHYMA and PROSENCHYMA were distinguished. By parenchyma was understood a tissue the cells of which were isodiametric or, if elongated in one direction, were separated by transverse walls. Prosenchyma was a tissue the elongated cells of which were spindle-shaped and pointed at both ends, which fitted between those of the associated cells. These two groups do not, however, suffice to give a survey of the variety of kinds of tissues, and the underlying conceptions are out of date, especially in the case of parenchyma.

On examining the tissues of the higher plants comparatively there is found in the first place a tissue which, like that composing the lowest multicellular plants, consists of cells with living contents and thin cellulose walls, and is capable of performing a diversity of functions; this will be termed PARENCHYMA. Other tissues may be sharply distinguished from this parenchyma by peculiarities of structure and special functions. The most striking tissues in the light of their main functions are the BOUNDARY TISSUE, the MECHANICAL TISSUE, and the CONDUCTING TISSUE. The PARENCHYMATOUS SYSTEM, the EPIDERMAL SYSTEM, the MECHANICAL SYSTEM, and the CONDUCTING SYSTEM correspond on the whole to these tissues. In addition the SECRETORY TISSUE and GLANDULAR TISSUE may be recognised.

The permanent tissues are frequently divided into epidermis, vascular bundles, and ground tissue.

1. Parenchyma. Parenchymatous System.—The parenchyma cell is characteristic of this type of tissue, the relative primitiveness of which has been referred to above (cf. p. 45). It may be isodiametric or elongated and of various shapes, and possesses the following further characters (cf. Figs. 3 *B*, 9, 40, 41). The cell wall, which as a rule consists of cellulose, is only moderately thickened and provided with simple round or elliptical pits; it thus facilitates the diffusion of substances from cell to cell. Living protoplasm is usually present, and the large vacuole may contain a considerable amount of nutritive material. The chromatophores, which have the form of chloroplasts or leucoplasts, often contain starch. Parenchyma is usually traversed by a ventilating system of intercellular spaces. Parenchyma may form part of other primary or secondary tissues and serves a variety of functions. The most important vital processes of the

full-grown plant take place in it, such as the preparation, conduction, and storage of nutritive materials, water storage, and the process of respiration. The presence of abundant cell sap contributes to the maintenance of the general rigidity of the plant body. The structural differences between parenchyma cells are relatively slight when the multiplicity of functions they perform are considered. When the cells have numerous chloroplasts they are spoken of as ASSIMILATORY PARENCHYMA (Fig. 8) in reference to their main function of forming organic substance from carbon-dioxide. The parenchyma of the subaerial parts of plants is often of this nature so far in as light can penetrate, while the deeper tissues are colourless. The term STORAGE TISSUE (Figs. 23 *A*, 24) is applied when these cells are rich in organic contents such as sugar, starch, fatty oils or proteids, or have hemicelluloses accumulated in the thickened walls (Fig. 39); these substances are stored against future use in the metabolism. WATER-STORAGE PARENCHYMA as a rule consists of large thin-walled cells with little protoplasm but abundant cell sap that is somewhat mucilaginous; these cells diminish in size on losing water. Conduction of organic food-materials, especially of carbohydrates, takes place in parenchymatous cells, which are elongated in the main direction of transport to facilitate this function. Such CONDUCTING PARENCHYMA often forms a sheath, without intercellular spaces, around other masses of tissue. Parenchyma which has large intercellular spaces, serving for ventilation or the storage of gases, is termed AERENCHYMA.

2. **Boundary Tissues.**—In the case of the multicellular tissues composing the bodies of land plants the whole body or particular tissues may require protection against excessive loss of water, mechanical injury, excessive heat (40), and frequently against the loss of diffusible substances. This function is carried out by cells which have certain peculiarities of structure and are often arranged in sheathing layers. In this way another group of tissues can be distinguished, the main elements of which are the epidermal cells and the suberised or cork cells. The epidermis together with some other types of cell form the epidermal system.

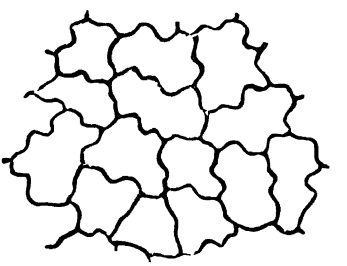


FIG. 48.—Surface view of the epidermis from the upper side of a leaf of *Mercurialis perennis*. (× 300. After H. SCHENCK.)

(a) Epidermal System. 1. EPIDERMIS.—This is derived from the superficial layer of the primary meristem (the dermatogen, cf. p. 86) and is thus one of the primary permanent tissues. It encloses the plant body as a protective investment while permitting exchange of materials with the environment. The epidermis is typically a single layer (Fig. 45 *B*) of tabular or more elongated living cells,

without intercellular spaces between them. The lateral walls are often undulated or toothed, which increases the firmness of the union of the cells. In transverse section the cells are of uniform depth and are rectangular or lens-shaped. The protoplasts of the epidermal cells are commonly reduced to thin layers lining the walls and enclosing large vacuoles filled with colourless or coloured cell sap. The epidermis of the parts exposed to light in most Ferns and in many shade-loving Phanerogams is provided with chlorophyll and takes part in assimilation. With progressive division of labour, however, chlorophyll is absent from the epidermis, which then serves merely to protect the more internal tissues especially against desiccation.

The outer walls of the epidermal cells of all subaerial parts of the plant, which last for a considerable time, are thickened. In this

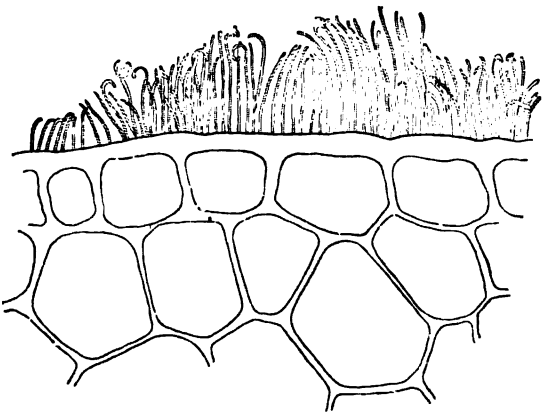


FIG. 44.—Transverse section of a node of the sugar-cane, *Saccharum officinarum*, showing wax incrustation in the form of small rods. (× 540. After STRASBURGER.)

respect they contrast with the epidermal cells of the more fugitive petals and of submerged and subterranean parts. This holds especially for roots in which the epidermis has very different functions, such as the absorption of water and salts. The thickening of the outer walls results from the apposition of cellulose layers, the outer of which usually, but not always, become more or less strongly cutinised (Fig. 190).

The outer walls of the epidermis, whether thickened or not, except in the case of those forming the surface of subterranean organs and especially roots, are covered by a thin continuous cutinised film called the CUTICLE. This is formed on the primary walls of the epidermal cells. The cuticle is often somewhat folded and in surface view appears striated. The cuticle and the cutinised layers of the wall are only with difficulty permeable to water and gases, and prevent the injurious loss of water by evaporation. The thickening also increases the mechanical

rigidity of the epidermal cells. On the other hand, the absence of cuticle from the root facilitates the absorption of water and salts from the soil. Deposits of wax are also present in the cutinised layers of the epidermis, and consequently water will flow off the epidermis without wetting it. The wax is sometimes spread over the surface of the cuticle as a wax covering. This is the case in most fruits, where, as is so noticeable on plums, it forms the so-called bloom. The wax coverings may consist of grains, small rods (Fig. 44), or crusts, soluble in ether or hot alcohol.

The epidermis may not only protect the more internal tissues from loss of water by hindering evaporation, but also by serving as a place of storage of water. The unthickened lateral walls of these cells become folded as the water is withdrawn

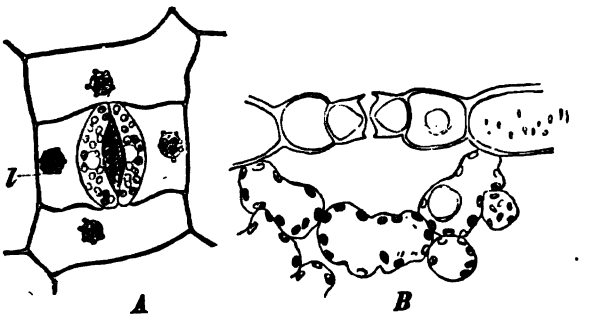


FIG. 45.—Epidermis from the under side of a leaf of *Tradescantia virginica*. *A*, In surface view. *B*, in transverse section; *l*, colourless rudiments of chromatophores surrounding the nucleus. (× 240. After STRASBURGER.)

from the cavity and stretch when the cell becomes again filled. Such an epidermis is frequently also composed of several layers of cells.

The mechanical strength of the outer walls of epidermal cells is increased in some plants by the deposition of calcium carbonate or of silicic acid. In the case of *Equisetum* the silicification is so great that the tissues are used in polishing tinware. The pericarp of the Grass, *Coix lachryma*, is almost as hard as the opal.

The epidermis of fruits, and particularly of seeds, exhibits a considerable variety of modifications in its mode of thickening and in the relations the thickening layers bear to one another. The purpose of these modifications in the epidermis becomes at once evident when it is taken into consideration that, in addition to protecting and enclosing the internal parts, the epidermis has often to provide for the dissemination and permanent lodgment of the fruits and seeds.

Among the ordinary cells of the epidermis there occur as a rule stomata and hairs which are especially characteristic of this tissue.

2. STOMATAL APPARATUS (41).—The presence of stomata in the epidermis is characteristic of most parts of the more highly organised plants that are exposed to the air. Each STOMA is an intercellular passage or pore bounded by a pair of curved, elliptical or half-moon-shaped cells called GUARD CELLS. The pore and guard cells together

constitute the STOMATAL APPARATUS (Figs. 45 *A*, 46). The largest stomata are found in grasses; thus in the wheat they measure 0·079 mm. in length by 0·039 mm. in breadth, while the pore itself is 0·038 mm. by 0·007 mm.

The PORE interrupts the continuity of the epidermis. It is an air-filled intercellular space opening below the epidermis into a large intercellular space (Fig. 45 *B*), which is spoken of as the respiratory cavity although it has nothing to do with respiration. This cavity is in communication with the intercellular spaces of the parenchyma. The stomata are of great importance to the plant, for they place the system of intercellular spaces, which serves to ventilate the tissues, in communication with the external atmosphere. This connection is necessary on account of the difficulty with which gases pass across the epidermis in order to renew the air in the intercellular spaces, and especially to replace the carbon-dioxide as this is used up. On the other hand, oxygen, which forms a considerable proportion of the air, can usually penetrate into the plant in sufficient quantity through the cuticle and the epidermal cells.

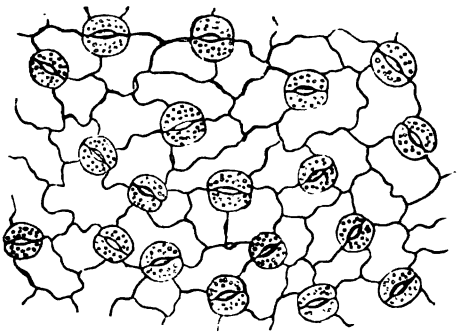


FIG. 46.—Epidermis with stomata from the lower surface of the leaf of *Helleborus niger*. (× 120. After STRASBURGER.)

The GUARD CELLS always contain chlorophyll and are characterised both by their shape and the manner in which their walls are thickened. This is best shown in transverse sections (Figs. 45 *B*, 47 *B*). There are usually an upper and a lower thickened band on the side of the guard cell which faces the pore, the portion of the wall between and the rest of the wall of the guard cell being relatively thin (Fig. 45 *B*). This structure stands in relation to the changes in form of the guard cells by means of which the size of the pore is varied. The pore is closed by a diminution of the curvature of the guard cells when there is danger of too great escape of moisture; while it is widely opened by increase in the volume of the guard cells and consequently of their curvature at other times. The stomata regulate the gaseous exchange and the transpiration.

As the transverse section in Fig. 45 *B* shows, the thickening ridges project both above and below the pore. There is thus an anterior chamber and a posterior chamber in relation to the narrow region of the actual passage. The thickened outer walls of the epidermal cells immediately adjoining the guard cells often have a thinner portion which acts as a kind of hinge and enables the changes

in shape of the guard cells to be effected without hindrance from the surrounding cells (cf. Fig. 47 *B*). The guard cells, as is seen in Fig. 45 *A*, are often surrounded by special cells called subsidiary cells; these may be less thickened or shallower than the other epidermal cells.

Differences are found in the construction of the guard cells and in the mechanism of opening and closure of the stoma which depends upon this. Two main types of stoma may be distinguished but they are connected by intermediate forms. In the first the change in form of the guard cells takes place mainly in the tangential direction, parallel to the epidermal surface; in the second in the radial direction at right angles to the surface. TYPE I.—According to the form of the guard cells the pore is opened in various ways. (*a*) The type of the Amaryllidaceae (Fig. 47) is found in the majority of Monocotyledons and Dicotyledons. The dorsal wall of each guard cell (Fig. 47 *B*) is unthickened, while the ventral wall (towards the pore) is thickened and usually shows the upper and lower thickening bands. When the cell becomes turgid the thin dorsal wall is more stretched than the thickened wall, and the cell, which in the flaccid condition was almost straight, becomes curved in the tangential plane to a semilunar shape. (*b*) The type of the Gramineae (Fig. 48) is met with in the Gramineae and Cyperaceae. The guard cells are dumb-bell-shaped; the widened ends being thin-walled, while the narrower middle region has both the outer and inner walls strongly thickened (Fig. 48 *B*). When the turgor increases the stiff middle portion of the guard cells are separated from one another by the expansion of the oval thin-walled ends of the cells. TYPE II.—*Mnium*-type (Fig. 49) is found in some Mosses and Ferns. In this the ventral walls of the guard cells are thin while the dorsal walls are thickened. When the turgor of the guard cell increases, the outer and inner walls are separated from one another, thus lessening the projection inwards of the ventral wall and opening the pore. The position of the dorsal wall remains unchanged.

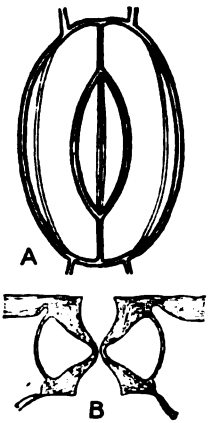


FIG. 47.

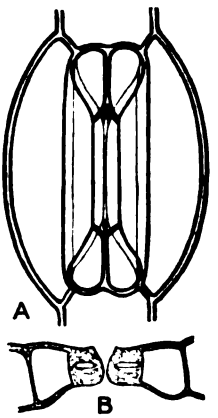


FIG. 48.

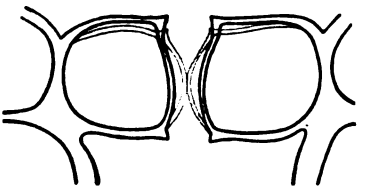


FIG. 49.

FIGS. 47-49.—Types of Stomatal Apparatus. The thick lines indicate the form of the guard cells in the open condition, the thin lines when the stoma is closed.

FIG. 47.—Type of the Amaryllidaceae. *A*, Surface view. *B*, In transverse section.

FIG. 48.—Type of the Gramineae with the two subsidiary cells. *A*, Surface view. *B*, Transverse section.

FIG. 49.—*Mnium*-type in transverse section. (After HABERLANDT.) Further description in the text.

The stomata are formed by the division of a young epidermal cell into two cells of unequal size, one of which, the smaller and more abundantly supplied with

protoplasm, becomes the stoma mother cell; while the larger, containing less protoplasm, usually forms an ordinary epidermal cell. The stoma mother cell becomes elliptical in outline and divides again, by a vertical wall, into the two guard cells, between which, by a splitting of the wall, the intercellular passage (pore) is formed. Before the formation of the definite stoma mother cell, successive divisions of the young epidermal cell often occur; in such cases the finally developed stoma is generally surrounded by subsidiary cells.

3. HAIRS. — The epidermis of almost all plants bears hairs (trichomes). They are sometimes unicellular structures and form papillate (Fig. 50), tubular (Fig. 51), or pointed (Figs. 52, 55, 56 to the left) protrusions of the epidermal cells. In other cases they are multicellular and form cell rows (Fig. 5), stalked or unstalked cell surfaces (scale-hairs, Fig. 54) which may resemble small leaves as in the ramenta of Ferns, or cell masses. The multicellular trichomes are also developed from young epidermal cells, and, indeed, usually proceed from a single initial cell of the hair by its growth and subdivision. Unicellular and multicellular hairs may further be unbranched or branched (Fig. 53, stellate hairs). Their walls may be

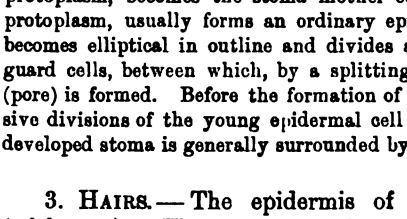


FIG. 50.—Surface of the upper epidermis of a petal of *Viola tricolor*, showing ridge-like infoldings of the lateral walls, and protruding papillae. (× 250. After H. SCHENCK.)

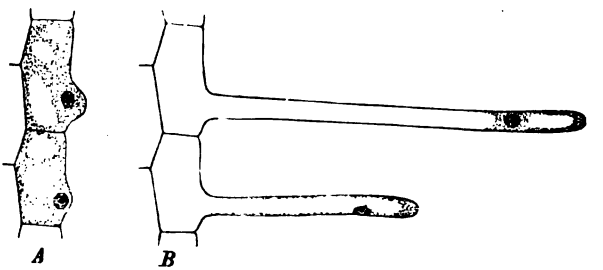


FIG. 51.—Epidermis of the root in longitudinal section showing root-hairs (*B*) and their origin (*A*). (After ROTHERT, semi-diagrammatic.)

thin and delicate or strongly thickened and frequently calcified or impregnated with silica, and sharply pointed at the tip (bristles, Fig. 55, right). The protoplasts may remain alive and resemble those of the epidermal cells, or may die. In the latter case the cavity often becomes filled with air and the hair appears white, or it may be laterally compressed as in the case of the long hairs of the cotton-seed (Fig. 52) from which the cotton of commerce is obtained. The basal portion of the hair in the epidermis may be distinguished from the

freely projecting body of the hair. The epidermal cells around the base are often arranged in a ring or radiate on all sides, and may be called the subsidiary cells of the hair. The STINGING HAIRS (Fig. 55), such as those of Nettles (*Urtica*) and of the Loasaceae, are special forms of bristles.

They arise from single epidermal cells which swell in the course of their development, and becoming surrounded by adjoining epidermal cells present the appearance of being set in sockets; while, at the same time, by the multiplication of the cells in the tissue at their base, the whole hair becomes elevated on a column-like protuberance. The hair tapers towards the apex and terminates, somewhat obliquely, in a small head, just below which the wall of the hair remains unthickened. As the wall of the hair is silicified at the end and calcified for the rest of its length, the whole hair is extremely stiff. The heads break off at the slightest

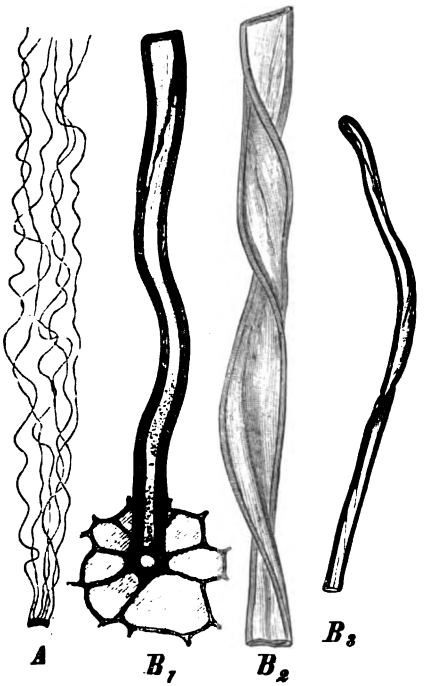


FIG. 52.—Seed-hairs of the cotton, *Gossypium herbaceum*. *A*, Part of seed-coat with hairs (× 3). B_1, Insertion and lower part, B_2, middle part, and B_3, upper part, of a hair. (× 300. After STRASBURGER.)

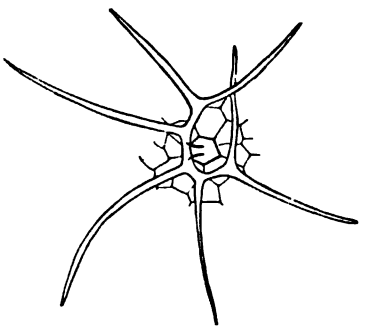


FIG. 53.—Stellate hair in surface view from the lower epidermis of the leaf of *Matthiola annua*. (× 90. After STRASBURGER.)

touch, and the hairs piercing the skin pour out their poisonous contents, which, especially in the case of some tropical nettles, may cause severe inflammation. According to G. HABERLANDT this is due to the presence of a toxin of albuminous nature.

Hairs have thus various forms and perform very different functions. They frequently contribute to the protection afforded by the epidermis, forming a covering to full-grown parts of the plant and very frequently to the young parts in the bud or expanding from this. Such coverings, which may be composed of dead woolly hairs, serve

to diminish the transpiration and are a protection against direct sunlight. The root-hairs (Figs. 51 *B*, 158 *r*) are tubular prolongations of living cells of the epidermis of the root and serve for absorption of water. Very diverse substances are excreted by glandular hairs (Figs. 75, 76, 77).

Certain hairs with abundant protoplasm and peculiar structure serve to receive mechanical stimuli according to G. HABERLANDT (43). They occur on stamens, petals, and the joints of leaves, and are known as tactile papillae, hairs, or bristles.

4. EMERGENCES, unlike hairs, are not formed solely by epidermal cells, but a number of cells, lying more or less deeply in the sub-epidermal tissues, also take part in their formation. They are sometimes glandular, and in other cases serve as organs of attachment.

Thus, for example, only a few rows of sub-epidermal cells enter into the formation of the emergences (Fig. 56) on

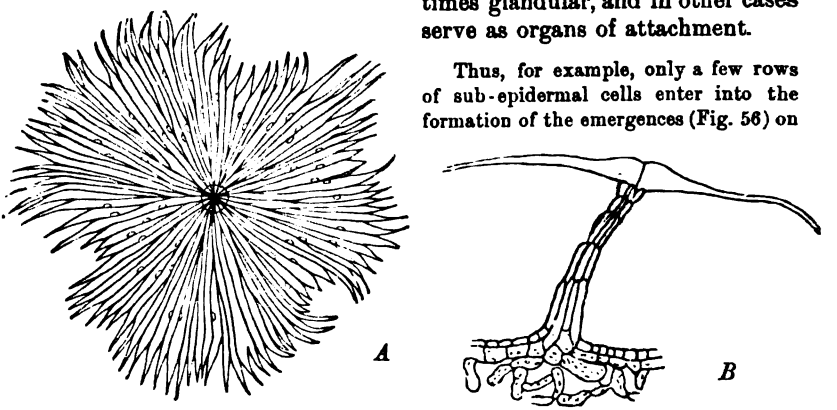


FIG. 54.—Scale-hair from the lower side of the leaf of *Shepherdia canadensis*. *A*, Surface view. *B*, Longitudinal section. (× 240. After STRASBURGER.)

the margins of the stipules of the Pansy (*Viola tricolor*), which are glandular. Deeper-lying tissue takes part in the construction of the anchor-shaped attaching organs, over 1 mm. long, which clothe the fruit of the Houndstongue (*Cynoglossum*) and lead to its dispersal by means of animals. The prickles of the Rose or Bramble are still larger emergences that are of assistance in climbing.

(b) Boundary Tissue formed of Corky Cells.—In many cases, and especially when the epidermis does not remain alive and functional during the life of the organ which it covers, the tissues of the body become limited and protected even more efficiently by suberised cells. Such cells also in the form of layers or sheaths serve to bound and delimit certain living masses of tissue from others within the plant body. Their origin may be primary or secondary. The suberisation is brought about by suberised lamellae being deposited on the pre-existing wall, while other layers of the wall frequently become lignified. Three kinds of suberised boundary tissues can be recognised: (1) The cutis tissue; (2) the endodermis; (3) the cork.

(1) The Cutis Tissue is a primary permanent tissue and arises by the early suberisation of cells of the epidermis or of thinner or thicker layers of parenchyma from which intercellular spaces are frequently absent. A tissue of the latter kind not uncommonly sheathes the outside of older parts of the plant (*e.g.* roots, Fig. 159 *ex*) or delimits strands of tissue within the plant from the surrounding tissue. The cells of this cutis tissue usually retain their living contents.

In place of suberisation the introduction of cutin or other substances that are imperfectly known chemically may render the membranes less permeable to water.

(2) Endodermis. — This tissue is formed of the endodermal cells (48). It very frequently encloses and bounds,

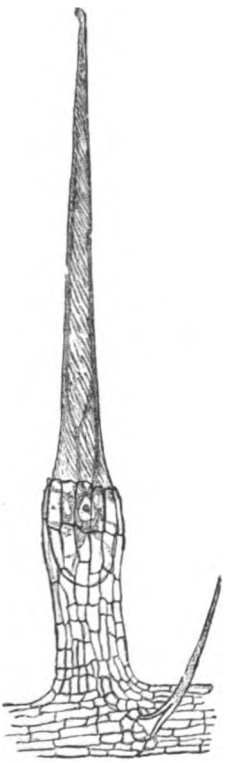


FIG. 55. — Stinging hair of *Urtica dioica*, with a portion of the epidermis, and, to the right, a small bristle. (× 60. After STRASBURGER.)

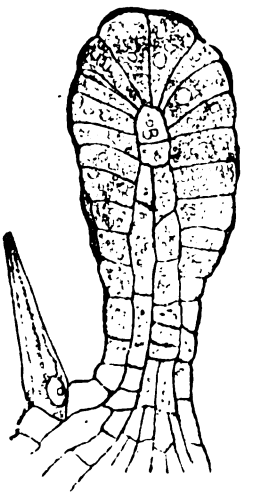


FIG. 56.—Glandular colleter from a stipule of *Viola tricolor*, showing also to the left a unicellular hair. (× 240. After STRASBURGER.)

as a sheath, a single layer of cells in thickness, living tissues within the plant, but it may also form a limiting layer on the outside. Its origin is sometimes primary and sometimes secondary. The elongated prismatic living cells of the endodermis have no intercellular spaces between them. When young the walls are not suberised, but a narrow strip of the membrane, in the form of a band running completely round the cell, has undergone a peculiar change by the introduction of an imperfectly known (? cork-like) substance (Caspary's band,

Fig. 57 *A*). This band gives the appearance of a dark dot or a dark lens-shaped body, Fig. 57 *B*, Fig. 161 *S*) in transverse sections, while it appears as an undulated band in radial longitudinal section. In older endodermal cells, as in the cells of the cutis, a secondary layer of corky substance is deposited all over the wall, and thick tertiary layers of carbohydrate material that often become strongly lignified may follow on this.

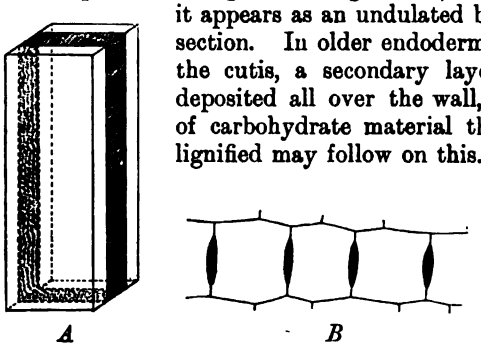


FIG. 57.—*A*, Diagrammatic representation of a single endodermal cell in the solid showing Caspary's band on the radial walls. *B*, Endodermis in transverse section; Caspary's band appears as the dark lenticular regions of the radial walls.

In the cutis tissue, when this is a single layer, and in the endodermis isolated cells, characterised by their shape and by their walls not being corky, frequently occur. These are known as transfusion cells.

(3) Cork.—While the epidermis and the cutis tissue are always primary permanent tissues the cork is always a secondary tissue, and is developed from a secondary meristem known as the CORK CAMBIUM. The cork forms either a thin peripheral layer a number of cells thick which is smooth and of a grey colour, or thicker fissured coverings of cork composed of radial rows of cells (Figs. 58, 59). It forms where the epidermis has been thrown off, or where living parenchyma has been exposed by wounds. The cork cells usually contain air and are brown, owing to the dead cell contents. They have a flattened prismatic form and are extended tangentially, fitting together without intercellular spaces. The secondary layers of the wall are suberised, while the middle lamella is often lignified. Tertiary thickening layers are either wanting or consist of cellulose forming the so-called cellulose layer which may sometimes become lignified. Even a thin layer of cork a few cells deep (Fig. 59) greatly diminishes the transpiration from the surface of any part of the plant, and, as will readily be understood, much more than the epidermis does. Thicker zones of cork also prevent the entry of parasites. Since cork is a poor conductor of heat it also protects the plant against over-heating.

Many old stems, tubers, bud scales, and fruits are covered with a layer of cork; thus the skin of a potato is of this nature. Bottle-cork is obtained from the Cork Oak.

The mature cells of cork are very rarely pitted, and either remain relatively thin (Fig. 58) or are more or less strongly thickened (Figs. 59, 185 *p*). Strongly thickened cork cells form what is known as STONE CORK. The cells of cork may be completely filled with dead contents (Fig. 59) which have usually a brown colour.

Frequently layers of suberised and unsuberised cells alternate in a corky tissue. The latter cells, which do not differ greatly from the cork cells in structure and

contents and may be thin- or thick-walled, arise in the same way and are called PHELLOID TISSUE. The BARK, which is met with on still older stems as the limiting tissue, consists of tissues of still more varied structure (cf. p. 163).

LENTICELS.—The formation of a covering of cork without intercellular spaces in place of the epidermis would prevent gaseous

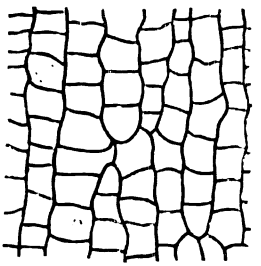


FIG. 58.—Transverse section of bottle-cork. (× 120.)

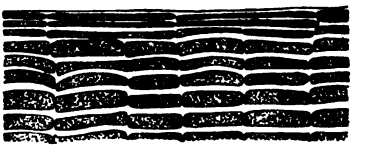


FIG. 59.—Transverse section of the cork layer of a Lime twig. The cell walls are left white, while the dead contents are dotted. (× 120.)

exchange between the interior of the stem and the atmosphere were the stomata not replaced in some way. This is effected in some plants (*e.g.* species of *Clematis*, *Vitis*, *Lonicera*) by porous cork, in

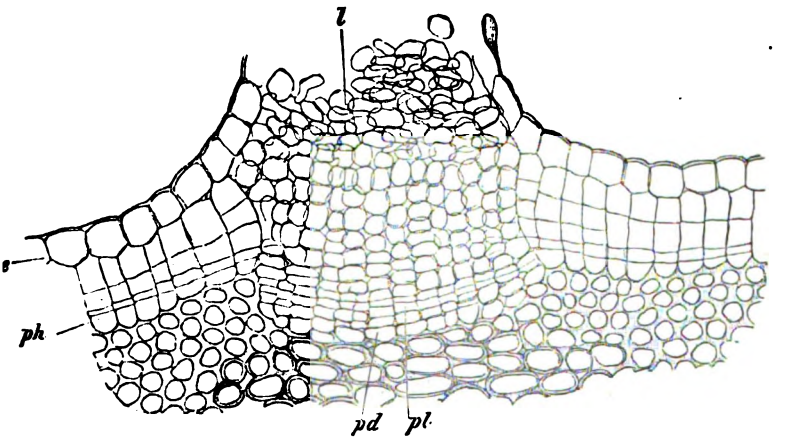


FIG. 60.—Transverse section of a lenticel of *Sambucus nigra*. *e*, Epidermis; *ph*, phellogen; *l*, complementary cells; *pl*, phellogen of the lenticel; *pd*, phelloderm. (× 90. After STRASBURGER.)

which small circumscribed oval or circular areas consist of somewhat smaller suberised cells with intercellular spaces between them. Usually, however, lenticels are present, rough porous warts elongated or spindle-shaped in outline which are readily seen by the naked eye on the cork of most trees. They consist of dead unsuberised tissue rich in intercellular spaces (COMPLEMENTARY TISSUE) interrupting

the layer of cork (Fig. 60). The intercellular spaces open on the one hand to the atmosphere, and on the other are in communication with the ventilating system of the underlying living tissues.

The lenticels frequently form beneath stomata and at an early stage in the development of the cork. The cork cambium which appears beneath the stoma has radially-running intercellular spaces between its cells (Fig. 60 *pl*), and forms to the outside complementary cells separated by intercellular spaces (Fig. 60 *l*). The lenticel soon breaks through the epidermis. Alternating with the complementary tissue the cork cambium in the lenticels forms layers of more closely-connected suberised and lignified cells (intermediate bands or closing layers). These are developed to close the lenticel during the winter and are again ruptured in the spring.

3. The Mechanical Tissue System (44).—Without a certain amount of rigidity the definite form which is essential to the performance of their functions in most plants would be inconceivable. In isolated cells and in growing tissues this rigidity is attained by turgor (cf. p. 225) and tissue tensions (cf. p. 286). Since, however, turgor and tissue tensions are destroyed by any great loss of water, leading to the wilting of the plant, they do not alone confer the necessary rigidity upon plants. We therefore find special tissues, known as the STEREOME, which have a purely mechanical function. These tissues are the SCLERENCHYMA and COLLENCHYMA.

How great are the demands made upon the stability of plants will be at once apparent from a consideration of a Rye haulm ; although it is composed of hundreds of thousands of small chambers or cells, and has a height of 1500 mm., it is at its base scarcely 3 mm. in diameter. The thin stems of reeds reach a height of 3000 mm. with a base of only 15 mm. diameter. The height of the reed exceeds by two hundred times, and that of the Rye haulm by five hundred times, the diameter of the base. In addition, moreover, to the great disproportion between the height and diameter of plants, they often support a heavy weight at the summit ; the Rye straw must sustain the burden of its ear of grain, the slender Palm the heavy and wind-swayed leaves (which in species of *Raphia* have a length of 15 m. and a corresponding breadth), while at times the weight of the bunches of fruit has also to be considered.

In plants, however, the rigid immobility of a building is not required, and they possess instead a wonderful degree of ELASTICITY. The Rye straw bends before the wind, but only to return to its original position when the force of the wind has been expended. The mechanical equipment of plant bodies is peculiar to themselves, but perfectly adapted to their needs. The firm but at the same time elastic material which plants produce is put to the most varied uses by mankind ; the wood forms an easily worked yet sufficiently durable building material, and the bast fibres are used in the manufacture of thread and cordage and textile fabrics (*e.g.* linen).

(a) Sclerenchyma.—This is the typical mechanical tissue of fully-grown parts of the plant and is formed of SCLERENCHYMA CELLS (stone cells) or SCLERENCHYMA FIBRES ("bast fibres"). Both when mature are as a rule dead cells with strongly thickened walls consisting

of lamellae of carbohydrate material, which is often lignified. The sclerenchymatous cells or stone cells (Fig. 30) are more or less isodiametric and polyhedral and have round, branched, or unbranched pits. The sclerenchymatous fibres (Fig. 61), on the other hand, are narrow, elongated, spindle-shaped cells with pointed ends, polygonal in transverse section (Fig. 62). They have obliquely-placed, narrow, elliptical pits. In their development sliding growth frequently occurs and they only mature in fully-grown parts of the plant. These elements may occur singly, but usually, especially in the case of the fibres, they are closely associated in strands, bands, rings, or sheaths, variously arranged so as to ensure the requisite rigidity of the organ against bending, tension, or pressure while employing the least mechanical tissue.

FIG. 61.—A sclerenchymatous fibre. (× about 100. After STRASBURGER.)

The firm thick walls of sclerenchymatous cells and fibres are not infrequently further hardened by deposits of mineral substances. The resistance which these forms of tissue offer when the attempt is made to cut, tear, or break them affords sufficient evidence of their hardness, tenacity, and rigidity.

Sclerenchymatous fibres have always a length which for a plant cell is considerable, on the average 1-2 mm. In some plants they are much longer, *e.g.* 20-40 mm. in Flax, to 77 mm. in the Stinging Nettle, and in *Boehmeria* even 220 mm. Such long fibres are of economic importance in the manufacture of textile fabrics. The long pointed ends render the connection of the fibres more intimate than is the case for the cells of other tissues.

SCHWENDENER has been able to determine their mechanical value by means of exact physical experiments and investigations. According to such estimates, the sustaining strength of sclerenchymatous fibres is, within the limits of their elasticity, in general equal to the best wrought iron or hammered steel, while at the same time their extensibility is ten or fifteen times as great as that of iron. It is true that soon after exceeding its limit of elasticity the stereome of the plant becomes ruptured, while the limit of rigidity for iron is not reached until the load is increased threefold. It is, however, of value for the needs of the plant that its limit of elasticity extends almost to the limit of its rigidity.

(b) Collenchyma. — The sclerenchyma corresponds to the bony skeleton of the animal body. Its elements are no longer in a condition which allows of growth, and it cannot be employed in parts of the plant which are still actively elongating. Where such parts of the plant require special strengthening in addition to that given by the tensions of cells and tissues, this is obtained by means of collenchyma.

The collenchymatous cells may be isodiametric but are usually elongated; they have transverse end walls (Fig. 64) or are pointed.

They resemble the cells of the parenchyma in being living cells, but differ in the unequal thickening of their cellulose walls. This is localised at the angles (angle collenchyma, Fig. 63) or on the tangential walls (surface collenchyma). Non-living inclusions, other than the large vacuole, are wanting in them. Intercellular spaces are absent or are very small. In spite of its high water-content collenchyma possesses a considerable rigidity against tearing owing to the thickening of the walls of its component elements. It at the same time allows and takes part in the growth of the organ, and may be regarded as the cartilaginous tissue of the plant. The distribution of the collenchyma is in relation to its mechanical functions. The extensive unthickened regions of the cell walls, which are further provided with round or elliptical pits, enable materials to be rapidly transported within this tissue.

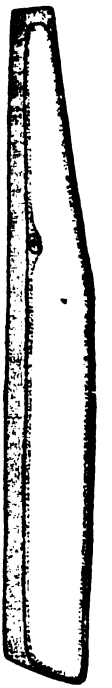


FIG. 64.—A collenchymatous cell seen from the side. (× 240.)

4. The Conducting Tissues.—As the body of

FIG. 62.—Transverse section of the sclerenchyma in the leaf of *Phormium tenax*. (× 240.)

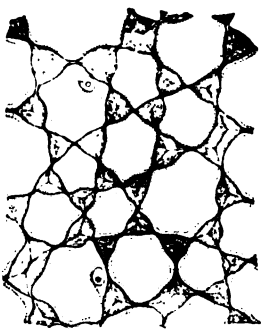


FIG. 63.—Transverse section of the collenchyma of *Cucurbita Pepo*. (× 240.)

a plant becomes larger and composed of more numerous cells, and especially as more parts of it project from the soil or water into the air, the need of rapid conduction of substances from one organ to another (*e.g.* from leaves to roots and conversely) increases. The movement of diffusion through the cross walls even of elongated parenchymatous cells does not suffice, though facilitated by the presence of pits in the wall and the complete suppression of intercellular spaces. Special conducting tissues have therefore arisen, the characteristically constructed elements of which are usually elongated in the main direction of conduction, frequently present enlarged surfaces for diffusion, and are further as a rule united to form con-

tinuous conducting channels. Such tissues are always associated in a connected system traversing the whole plant.

(a) Sieve-Tubes.—The elements composing the SIEVE-TUBES [45] are arranged in longitudinal rows and connected by open pores which appear to serve for the transport of proteids and carbohydrates. The transverse or oblique ends, and sometimes the lateral walls, have sieve-like perforated regions the pores of which are filled with thick protoplasmic strands. These are called the SIEVE-PLATES (Fig. 65 *A*, *B*). In many plants (*e.g.* the Cucumber, Fig. 65 *A*) the entire transverse wall forms one area perforated by relatively coarse pores.

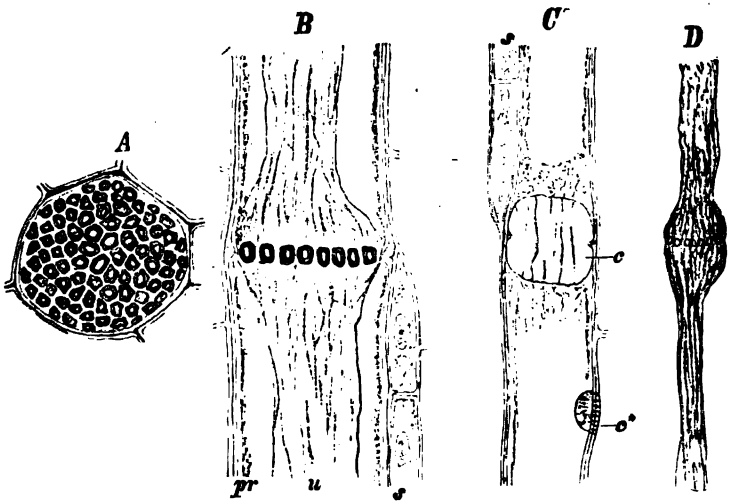


FIG. 65.—Parts of sieve-tubes of *Cucurbita Pepo*, hardened in alcohol. *A*, Surface view of a sieve-plate. *B*, *C*, Longitudinal sections, showing segments of sieve-tubes. *D*, Contents of two sieve-tube segments, after treatment with sulphuric acid. *s*, Companion cells; *u*, mucilaginous contents; *pr*, peripheral cytoplasm; *c*, callus plate; *c**, small, lateral sieve-plate with callus. (× 540. After STRASBURGER.)

On the longitudinal walls the sieve-plates have the form of narrowly circumscribed circular areas with much finer pores (Fig. 65 *C*, *c**) where two sieve-tubes adjoin laterally. In other cases several finely-perforated areas (sieve-plates or SIEVE-PITS) are found on the oblique end wall of a sieve-tube (Fig. 66). The elements of a sieve-tube (Fig. 65), each of which corresponds to a cell, contain a thin living protoplasmic layer lining the wall, with a single nucleus, leucoplasts, and often starch grains. This encloses a watery, alkaline, more or less concentrated, and coagulable cell sap which is rich in albuminous substances and frequently in carbohydrates and inorganic salts (phosphates). The walls of sieve-tubes are almost always unlignified; they consist of cellulose and are elastically stretched by

their contents. As a rule they remain functional during one vegetative period only. Before passing into the inactive condition their sieve-plates become covered by highly refractive plates of CALLUS (Fig. 65 *C*), which diminishes or prevents the exchange of materials between the members of the sieve-tube. If the sieve-tube resumes its function in the succeeding vegetative period this callus is again dissolved.

The callus plates consist of CALLOSE, a substance the chemical composition of which is still unknown; this is characterised by its insolubility in ammonia-oxide of copper and its solubility in cold 1 % solution of potash. It is coloured reddish-brown by chlor-zinc-iodide, a shining blue with aniline blue, and shining red with corallin (rosolic acid).

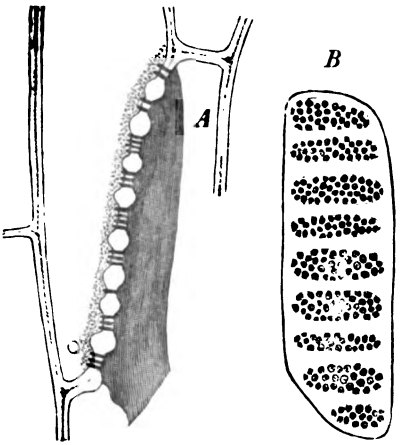


FIG. 66.—*A*, Junction of two elements of a sieve-tube of *Vitis vinifera*, the oblique wall being shown in section. (× 600. After DE BARY.) *B*, A similar wall in surface view showing the sieve-pits. (Diagrammatised by ROTHERT after DE BARY.)

(b) Vessels.—Special, and ultimately dead, cells, which are tube-like with a circular or polygonal cross-section and are elongated and arranged in longitudinal rows in the main direction of conduction, serve for the conduction and storage of water in the plant. The lignified walls of these vessels have striking and characteristic thickening. So long as they are functional the vessels contain water, and often also a limited amount of air. They are distinguished as TRACHEIDES and TRACHEAE. The tracheides are single cells with pointed ends, and are as a rule of narrow diameter. Their walls bear peculiar pits (Fig. 70 *B*). These elements frequently serve as mechanical tissue, as in the stems of Coniferae. The tracheae, on the other hand, are wider or narrower tubes formed from a number of cells by the disappearance of their end walls. When the latter are transversely placed they are completely dissolved, leaving only a narrow annular rim which becomes further thickened (Figs. 67 *C*, *s*, 69 *I. q*, *q'*). Obliquely placed, end walls, on the other hand, are usually not pierced by a single large opening but by a number of elliptical openings placed one above the other (scalariform perforation, Figs. 69 *II.*, 173 *tg*). Some of the end walls are not perforated but merely pitted, and the vessels are thus of limited length.

Some tracheae, in particular those of woody climbers or lianes, may be some metres in length. In the Oak also tracheae two metres in length are frequent. As a rule, however, they do not exceed 1 m. and are usually only about 10 cm. in

length. The widest as well as the longest vessels are met with in climbing plants; in them they may be 0·7 mm. wide, while those of the Oak are about 0·25 mm. and of the Lime 0·06 mm.

The terminology of the water-conducting elements is somewhat confused in the literature. As a rule the distinction is drawn between tracheides and tracheae or vessels. DE BARY, however, called all these elements tracheae and distinguished between tracheides and vessels. The suggestion of ROTHERT which is adopted here appears most convenient, viz. to distinguish within the collective conception vessels, the tracheides and tracheae.

The thickening of the walls of vessels may have the form of narrow bars, T-shaped in cross-section (Fig. 68) on the relatively thin

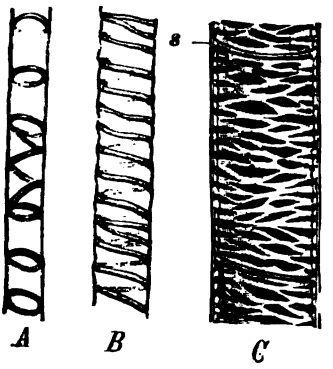


FIG. 67.—*A*, Part of an annular tracheide. *B*, Part of a spiral tracheide. *C*, Longitudinal section through part of a reticulate trachea showing the remains of a partition wall, *s*. (× 240. After H. SCHENCK.)

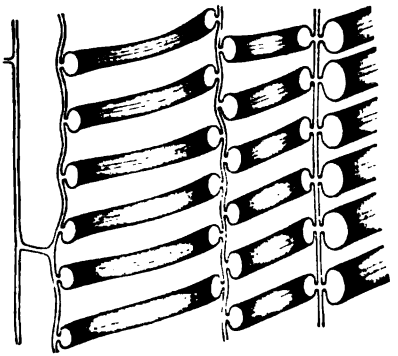


FIG. 68.—Portion of a longitudinal section through three spiral vessels and a row of parenchyma cells of the Gourd (*Cucurbita Pepo*). (× 560. After W. ROTHERT.)

wall. These bars may form isolated rings, connected spirals, or a network, and accordingly ANNULAR, SPIRAL, and RETICULATE tracheides and tracheae are distinguished (Figs. 67, 68). In other cases the thickening involves the greater part of the cell wall but leaves numerous pits (PITTED VESSELS, Figs. 69, 70). The pits may be circular, polygonal, or more or less transversely extended and elliptical or slit-like. When transversely-extended pits stand above one another in regular rows on the lateral walls the vessel is termed SCALARIFORM (Fig. 69 *II.*, 70 *A*). The pits of pitted vessels are always BORDERED PITS (40), the canal of which widens from the cell lumen to the pit membrane (Fig. 71). They may be present on one or both sides of a cell wall. The outline of the pit in surface view is commonly circular and encloses a smaller circle (Fig. 71 *A*). The smaller circle is the opening into the cell cavity, while the wider outline is that of the pit cavity at its widest part adjoining the pit membrane. The thickening of the cell wall thus overhangs the pit membrane and forms the wall of the pit, between the outer and

inner circles. The pit membrane is frequently thickened in the centre forming the TORUS (Fig. 71 *C*), and this, when the membrane is deflected to one or other side, may close the entrance like a valve (Fig. 71 *B*, *t*). The wide membrane of the bordered pits allows readily of movements of water from the one cell cavity to the other, while the overhanging

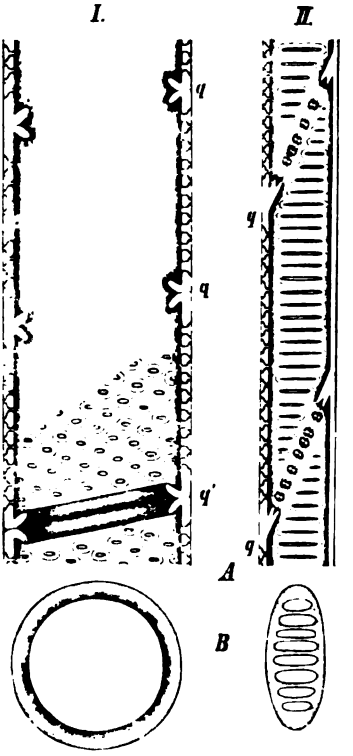


FIG. 69.—*A*, Diagrams of tracheae in longitudinal section. *I.*, Wide trachea with small elliptical bordered pits, and with simple perforation of the end wall (*q*, *q*). The further portion of the wall is cut away in the upper portion of the figure. *II.*, Narrow trachea with scalariform pitting of the wall and perforation of the transverse wall, *q*. *B*, The transverse walls of the two tracheae in surface view. (After ROTHERT.)

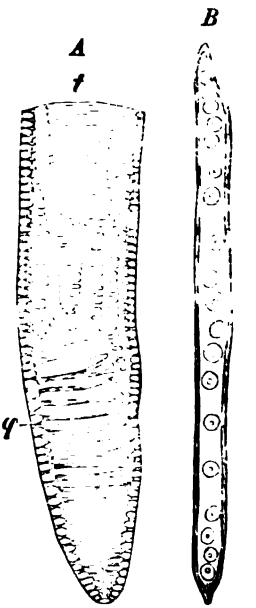


FIG. 70.—*A*, Lower third of a scalariform tracheide from the rhizome of the Bracken Fern (*Pteris aquilina*); *t*, the transversely-extended pits on the lateral walls; *q*, the scalariform pitted end wall. (× 95. After DE BARY.) *B*, A tracheide with circular bordered pits. (× 100. After STRASBURGER.)

wall of the pit ensures that the rigidity of the wall is not unduly diminished.

As Fig. 71 shows, the pits are bordered on both sides of a wall separating two water-conducting elements. When, however, a vessel abuts on a living cell, the pit is only bordered on the side of

the membrane toward the water-conducting element and the pit membrane has no torus. On the other side of the wall a simple pit is developed.

There are transition forms between the various types of vessels, and the thickening bands, in annular and spiral vessels, correspond to the walls of the bordered pits.

These thickening bars are in fact, as was mentioned above, always narrowed at their attachment to the wall (Fig. 68). As a result of this they are readily detached from the unthickened membrane in the preparation of sections, the spiral thickening often lying within the cavity. The thin portions of the wall between the thickenings correspond to the pit membranes, and, when occurring between two water-conducting elements, may be somewhat thickened like a torus.

Annular or spiral vessels are formed in growing parts of plants as they can undergo extension or stretching.

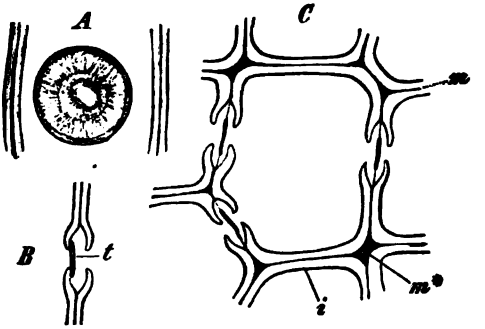


FIG. 71.—Tracheides from the wood of the Pine, *Pinus sylvestris*. *A*, Bordered pit in surface view. *B*, Transverse section of bordered pit from a tangential section of the wood; *t*, torus. *C*, Transverse section of a tracheide; *m*, middle lamella, with gusset, *m**; *i*, inner peripheral layer. (× 540. After STRASBURGER.)

The thickening of the walls of water-conducting elements increases the mechanical rigidity of the latter and prevents their being crushed by the adjoining living cells. The living contents of the vessels diminish as the wall thickens and ultimately completely disappear. This does not happen in the tracheae until after the transverse walls have been broken through.

System of Tissue of the Vascular Bundles.—The sieve-tubes are usually associated with conducting parenchyma to form strands or bundles of phloem which traverse the plant. The same holds for the tracheides and tracheae, although isolated or grouped tracheides may occur as a water-storage tissue in the parenchyma. Such strands of phloem or of vascular tissue may be regarded as INCOMPLETE VASCULAR BUNDLES. They are common in the secondary permanent tissue as vascular strands in the wood and phloem strands in the bast (cf. pp. 154, 159). In the primary tissues, however, the phloem and vascular strands are united to form COMPLETE VASCULAR BUNDLES which run as a rule parallel to the long axis of an organ, and are united by cross connections into a network. The name VASCULAR BUNDLE SYSTEM is given to this striking feature in the construction of a plant. In these bundles the elements which serve for the conduction of water are associated with those which conduct organic

material, so that these different substances follow nearly the same course though usually in opposite directions. This tissue system may in its origin be primary or secondary.

Such complete vascular bundles contrast with the less dense surrounding tissue by the narrowness of their elements, and the absence of intercellular spaces; they are often visible to the naked eye as in the translucent stems of *Impatiens parviflora*. Strands of tissue of two sorts are to be distinguished in each bundle, the vascular portion or XYLEM, and the sieve-tube portion or PHLOEM. The xylem and phloem may be variously arranged in the bundles, the transverse sections of which differ accordingly (cf. p. 99).

FIG. 72.—Portion of a laticiferous cell of *Ceropegia*. (× 150. After STRASBURGER.)

Other names are used in the literature for the complete conducting bundle and its parts. Thus the conducting bundles are also termed vascular bundles, fibro-vascular bundles, or mestome; the xylem is spoken of as the woody portion, vascular portion, or hadrome; and the phloem as bast or leptome.

5. Secretory Cells and Secretory Tissue. (1) SOLITARY CELLS.—Secretory cells isolated or arranged in rows are of frequent occurrence in the most diverse tissues. They may be isodiametric or tubular, and contrast with the other cells by reason mainly of their contents. Within their diminished or dead protoplasts secretions of the most varied kinds are contained. These are end products of the metabolism and may have an ecological significance as protective substances. Mucilage, gums, ethereal oils, resin, gum-resin, tannin, alkaloids, and crystals of oxalic acid (Fig. 22) are among the most frequent secretions. The walls of these cells are often suberised.

The non-septate LATICIFEROUS CELLS which contain the secretion called LATEX belong here. They are richly-branched tubes without cross walls, with a smooth elastic cellulose wall that is usually unthickened (Fig. 72). They have a layer of living protoplasm with numerous nuclei lining the wall and sometimes contain starch grains ([47]), which in many Euphorbiaceae are dumb-bell-shaped. Their cell sap is a milky, usually white, watery fluid which rapidly coagulates on exposure to the air.

Enzymes (in *Ficus Carica* and *Carica Papaya* peptonising enzymes in addition), tannins, poisonous alkaloids, and especially calcium-malate, occur dissolved in the latex. As droplets in an emulsion gum-resins (mixtures of gum and

resin), caoutchouc, gutta-percha, fats and wax occur, and as a solid constituent proteid granules.

The laticiferous tubes in Euphorbiaceae, Moraceae, Apocynaceae, and Asclepiadaceae proceed from cells which are already recognisable in the embryonic plant, and with the growth of the latter continue to grow, branch, and penetrate all the organs so that they may become many metres in length.

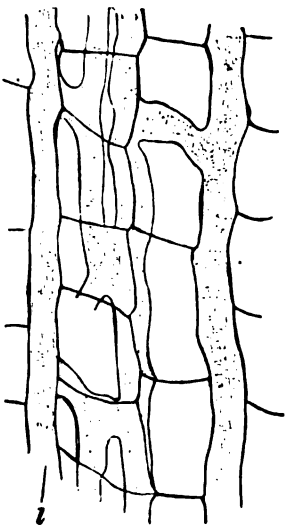


FIG. 73.—Tangential section through the periphery of the stem of *Scorzonera hispanica*, showing reticulately-united latex vessels. (× 240. After STRASBURGER.)

(2) CELL-FUSIONS. — A number of secretory cells may unite to form a more spacious reservoir for the secretion, by the dissolution of the walls between them. This is most strikingly seen in the LATICIFEROUS VESSELS. They resemble the laticiferous cells in appearance and in their contents, but differ in their origin by the fusion of a number of cells forming a network (Fig. 73). Remains of the transverse walls may be recognised in this.

The laticiferous vessels, like the laticiferous cells, are limited to certain families of plants, for instance the Papaveraceae (*Papaver*, *Chelidonium*, with reddish-orange latex), the Campanulaceae, and in the Compositae the Cichorieae (*Cichorium*, *Taraxacum*, *Lactuca*, *Scorzonera*, *Hieracium*, *Tragopogon*).

There is little ground for the widespread idea that the laticiferous cells and vessels also assist in the transport of materials.

The MUCILAGE TUBES which occur in many Monocotyledons are in many respects similar to the laticiferous vessels. Their mucilaginous sap consists of albumen, starch, glucose, tannins, and inorganic substances.

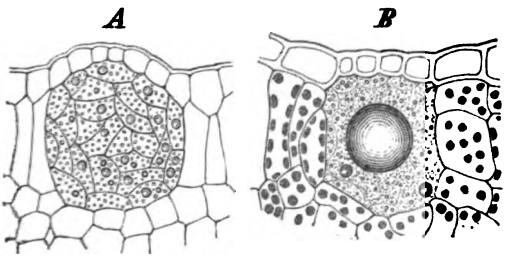


FIG. 74.—Lysigenous oil-reservoirs from the leaf of *Dictamnus fraxinella*. *A*, Young. *B*, Mature after dissolution of the cell walls. (ROTHERT altered from RAUTER.)

(3) LYSIGENOUS INTERCELLULAR SPACES. — Secretory reservoirs frequently arise as spherical, irregular, or tubular cavities by dissolution of entire secretory cells, *i.e.* lysigenously (Fig. 74).

These lysigenous secretory reservoirs arise from groups of cells in

which the secretion has been formed and the walls gradually dissolved. The secretory cavities filled with ethereal oils in the orange and lemon have this origin.

6. Glandular Cells and Glandular Tissue. — Glandular cells, which excrete substances from their protoplasts to the outside or into the intercellular spaces, occur singly or in groups in the epidermis, in

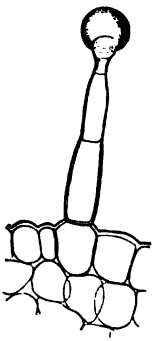


FIG. 75. — Glandular hair from the petiole of *Primula sinensis*. (× 142. After DE BARY.)

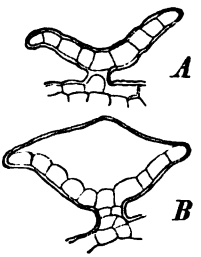


FIG. 76. — Glandular scale from the female inflorescence of the Hop, *Humulus lupulus*, in vertical section. *A*, before, *B*, after the cuticle has become distended by the secretion. In *B* the secretion has been removed by alcohol. (× 142. After DE BARY.)

the parenchyma, and in other tissues. The glandular cells resemble parenchymatous cells, but have as a rule abundant protoplasm and large nuclei as in meristematic cells. The excreted substances are usually end products of metabolism and frequently have an ecological significance. Closely connected glandular cells forming a layer constitute a GLANDULAR EPITHELIUM.

Glandular epithelia or isolated glandular cells are of frequent occur-

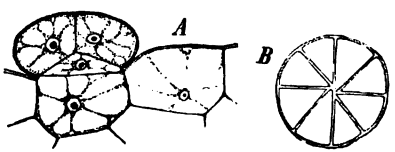


FIG. 77. — Sessile digestive gland from the upper side of the leaf of *Pinguicula vulgaris*. *A*, In longitudinal section. *B*, Seen from above. (ROTHERT altered from FENNER.)

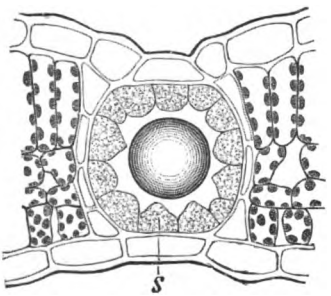


FIG. 78. — Schizogenous oil-reservoir in a cross-section of the leaf of *Hypericum perforatum*. *S*, the glandular epithelium. (After HABERLANDT.)

rence in the epidermis and are often covered by a porous cuticle. In this situation glandular hairs, the knob-shaped end cell of which is secretory (capitate hairs, Fig. 75), also occur. Other glandular hairs may be scale-shaped (Fig. 76), and glandular emergences (Fig. 56) are also found. The secretion is very often composed of resinous

substances, and accumulates between the outer wall of the secretory cells and the cuticle which is raised up and finally burst. The same holds for the formation of other adhesive substances and mucilage.

According to the excreted products, which may have varied ecological uses, the epidermal glands may be distinguished into mucilage, oil, resin, digestive (Fig. 77) glands, also salt glands, water glands (hydathodes), and nectaries ([48]). The last-named secrete a sugary fluid which attracts insects and occur as glandular surfaces or hairs within the flower or in other situations (cf. Fig. 136 *n*). These are termed respectively floral and extra-floral nectaries.

The glandular cells or epithelia enclosed within parenchymatous or other tissues always abut on circular or irregular intercellular spaces or tubular, branched, or unbranched canals which sometimes run through the whole plant as a connected system of tubes. These intercellular spaces, which arise by the splitting apart of cells, form the schizogenous secretory reservoirs (Fig. 78). Their contents consist of ethereal oils, resin, gum, or mucilage, and corresponding distinctions are made in naming these canals.

Schizolysigenous reservoirs also occur.

SECTION III

ORGANOGRAPHY ([49])

THE EXTERNAL MEMBERS AS ORGANS OF THE PLANT

THE organisms included in the vegetable kingdom are variously shaped and segmented. Some are unicellular throughout life, while others are multicellular. Both may have very simple and regular geometrical forms and have no external segmentation, or on the other hand may possess a body with a very irregular outline owing to its being divided into protrusions of the most various kinds.

I. Significance of the External Segmentation to the Organism.—The construction and segmentation of any particular organism stand as a rule in close relation to its needs and mode of life. The external as well as the internal segmentation is usually the expression of a DIVISION OF LABOUR between the parts or the cells of the multicellular body. The external members are, in fact, usually ORGANS with definite vital functions. The physiological progression from simpler to more segmented organic forms consists in great part in the increase of this division of labour.

II. Main Groups of Organs.—The activity of every organism has two sides. It must nourish itself in order to maintain itself as an individual, and it must reproduce in order that the race should not perish with its death. The body of the plant subserves these two fundamental vital impulses. Only in primitive plants does the whole

mass serve both equally; usually certain parts are concerned with the nutritive processes and others with reproduction. There is thus usually a clear division of labour between the vegetative organs and the reproductive organs, which are fundamentally different in form and structure as well as in function. These two groups of organs will require separate consideration.

III. Relations of Symmetry.—The form of the whole segmented or unsegmented organism and of its parts is determined by their relations of symmetry. Like nearly all properties of organic forms this is closely connected with the mode of life of the organism, especially with the direction of growth of the plant and the position of its members in space. As a rule, therefore, the symmetry of the internal construction of a plant corresponds to that of its external form.

Apart from a few very simple forms, the plant body and its individual parts nearly always exhibit POLARITY and a distinction of base and apex. Such a distinction is shown both in free motile forms, in which the direction of progression is usually determined by the polar construction of the body, and in attached forms, where the organism is attached to the substratum by its basal pole.

Every section through a part of a plant parallel to the longitudinal axis is a longitudinal section. When it passes through the axis it is termed a radial longitudinal section, and when it is at right angles to a radius but not in the plane of the axis itself a tangential longitudinal section. Sections at right angles to the long axis are transverse sections. An organism or a part of a plant which is almost similarly constructed around its longitudinal axis is termed RADIAL or ACTINOMORPHIC (Fig. 525 *A*). Such a structure can be divided by a number of radial longitudinal sections into approximately equal halves, which are mirror images of one another; it has thus a number of PLANES OF SYMMETRY. When there are only two planes of symmetry standing at right angles to each other the structure is called BILATERAL (Fig. 107). Lastly, when there is only a single plane of symmetry (the MEDIAN PLANE) the structure is DORSIVENTRAL or ZYGOMORPHIC; the two lateral halves correspond, while the anterior and dorsal sides are unlike (Fig. 525 *B*). Plants or parts of plants which grow vertically upwards or downwards (ORTHOTROPOUS) are usually radial or bilaterally symmetrical. When, on the other hand, they grow oblique or at right angles to the vertical (PLAGIOTROPOUS) they are frequently dorsiventral. There are also ASYMMETRICAL organic structures, which cannot be divided by any plane into corresponding halves. Some dorsiventral structures, *e.g.* leaves, become asymmetrical by the one half being differently formed to the other. This is, for example, the case with the leaves of Begonia, and in a less degree with those of the Elm. The whole radially symmetrical plant body is here composed of dorsiventral and asymmetrical parts.

I. Vegetative Organs

The highest segmentation attained by the vegetative organs of plants is that into ROOT, STEM, and LEAVES. Stem and leaves are classed together as the SHOOT. A plant body composed of shoot and root is termed a CORMUS, and plants so constructed CORMOPHYTES. The fern-like plants, or Pteridophyta, and the more highly-segmented seed plants derived from them are cormophytes.

The cormophytes arose phylogenetically from more simply organised plants in which the plant body had not attained such a profound segmentation; in which roots were wanting, while leaf-like branches though not true leaves were present. Such structures, as well as quite simple and unsegmented plant bodies, are included under the term THALLUS, and such plants may be contrasted with the cormophytes as thalloid. The Algae, Fungi, Lichens, and all Bryophyta have thalli.

The thalloid plants must not be confused with the Thallophyta. All thalloid plants possess a thallus, but they are not all Thallophyta. Under this name systematic botany includes only the Algae, Fungi, and Lichens.

A. THE THALLUS (50)

(a) Algae, Fungi, Lichens. 1. Simplest Forms.—The only forms that are quite unsegmented externally are a number of microscopically small unicellular or multicellular plants. The simplest form that can be assumed by an organism is that of the sphere.

For example, such spherical cells are shown by some Algae that form a green coating on damp walls (Fig. 35), and by many Bacteria (Fig. 80 *b*). The latter include by far the smallest known organisms.

2. Increase of Surface.—Of all geometric figures the sphere has the smallest surface for the same volume, and this surface bears a smaller ratio to the volume the greater the latter is. Deviations from the spherical form are thus connected with a relative increase of the surface. In particular, as the volume of the body increases the surface area is in this way increased relatively to the volume. Cylindrical, rod-shaped, filamentous, ribbon-shaped, and discoid forms thus occur, and ultimately bodies segmented by reason of their external projections. The free surface of the body is of great importance to the plant for the absorption of the gaseous and liquid substances necessary for its nutrition and derived from the environment.

Even when spherical the cells of Bacteria on account of their minute size have an extraordinarily large free surface as compared with cells of higher organisms.

The unicellular individuals of the beer Yeast (cf. Fig. 20) are ellipsoidal in shape, while the cells of many Algae, such as species of Diatoms (Fig. 79), are discoid or cylindrical. This group of Algae exhibits spindle, canoe, helmet, and

fan shapes, and also filamentous ribbon- and chain-like forms. Rod-shaped and spirally-wound forms are met with in the Bacteria (Fig. 80 *a*, *c*, *d*).

Such living beings may be attached by mucilage to a substratum or may float free in water. The free-floating organisms of continental water surfaces as well as of the ocean are termed PLANKTON in contrast to the firmly-attached aquatic organisms which constitute the BENTHOS. The plankton flora, which is rich in peculiar species, contains such forms as have been mentioned above. These may have the power of active movement (swimming forms) due as a rule to projections of the protoplast as slender contractile flagella or cilia which are special organs of locomotion. This power of movement enables many organisms of the plankton, responding to stimuli, to seek for favourable nutritive conditions or to avoid unfavourable spots. Other forms of the plankton are suspended without true power of movement in the water

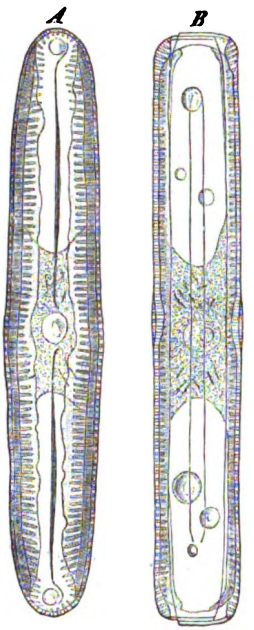


FIG. 79.—*Pinnularia viridis*. *A*, Surface view. *B*, Lateral view. (× 540. After STRASBURGER.)

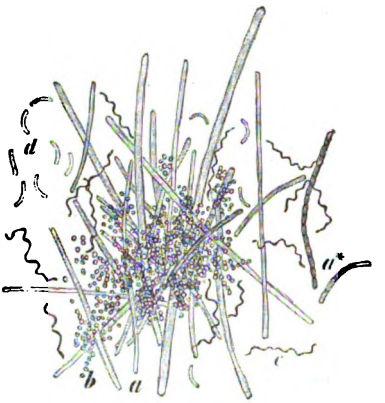


FIG. 80.—Bacteria from deposits on teeth. *a*, *Leptothrix buccalis*; *a**, the same after treatment with iodine; *b*, *Micrococcus*; *c*, *Spirochaete dentium* after treatment with iodine; *d*, *Spirillum sputigenum*. (× 800. After STRASBURGER.)

(floating forms). Many of them, and other plankton organisms, show special arrangements for flotation in the increase of body surface by long bristles, bars, and plates. The friction of the body against the water is thus considerably increased and sinking made more difficult (51).

3. Establishment of Polarity.—The next stage in progressive complexity of form is the establishment of the distinction between base and apex. In freely motile forms the cilia are frequently attached at one pole. In fixed forms one pole forms an ORGAN OF ATTACHMENT, as, for instance, a circular disc of attachment or palmately-branched lobes. The further growth may at the same time be restricted to a small region of the body or GROWING POINT. This

in intercalary growth is a zone between the base and apex, while in apical growth it is situated at the summit of the plant body. A young plant of the green seaweed *Ulva lactuca* affords an example of the latter condition (Fig. 81).

4. Flattening.—Many Algae and Lichens have a disc-shaped or ribbon-shaped thallus (Fig. 83) by which the free surface is further increased. The assumption of this form may therefore be regarded as an adaptation to the nutritive relations of the organism. The latter constructs its organic substance from the carbon dioxide which it can decompose, but this process of assimilation only takes place in plants that contain chlorophyll and in the light. Thus as many chlorophyll grains as possible require to be exposed to the light, and this is attained even in massive bodies by flattened form.

5. Dorsiventrality.—The majority of the forms so far referred to are radial or bilaterally symmetrical. In those in which the thallus spreads out on a substratum (*e.g.* in many Lichens), the construction of the plant body further becomes dorsiventral. Dorsiventral symmetry is characteristic of forms in which the upper side is the more strongly illuminated and is especially concerned in assimilation.

6. Branching. — Filamentous, ribbon-shaped, and discoid forms, the surface of which is extended as branches, are still more highly organised. This occurs in most thalli of Algae, Fungi, and Bryophyta. The free surface is still further increased by the branching, and the available space is better utilised. Thus bushy, shrub-like, and dendroid thalli arise; these in the Algae have often delicate branches moving with the surrounding water to which they offer little resistance.

FIG. 81.—*Ulva lactuca*, young stage, showing apex and base. (× 220. After STRASBURGER.)

In branching the apex of the young plant may divide into two new and equivalent parts (DICHOTOMOUS BRANCHING), as happens repeatedly in the fan-shaped thallus of the Brown Seaweed, *Dictyota dichotoma* (Fig. 83; cf. the diagram in Fig. 82 *a*). In other branched forms there is a new formation of growing points which give rise to lateral branches (LATERAL BRANCHING), and in the higher forms this becomes more and more limited to the apical region of the thallus; the youngest and shortest lateral branches are the nearest to the apex. Such an ACROPETAL origin of new lateral members is already evident in the filamentous Green Alga, *Cladophora* (Fig. 84; cf. also Fig. 89). In the simplest case of lateral branching a single main axis (MONOPODIUM) continues its apical growth throughout the branch system. It behaves as the parent axis to a large number of

lateral axes, arising successively on all sides. These grow less actively than the main axes but can in turn branch similarly. This type of branching is called racemose (cf. the diagram, Fig. 82 *b*).

All lateral axes which arise on the axis of the young plant are

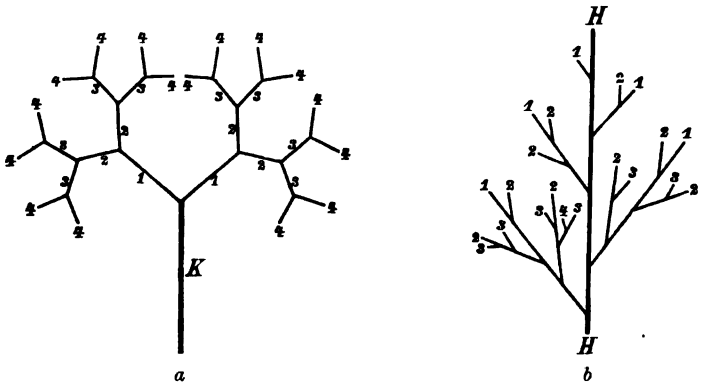


FIG. 82.—*a*, Diagram of dichotomous and, *b*, of lateral racemose branching. *K*, Axis of the young plant; *H*, main axis; *1*, *2*, *3*, *4*, lateral axes of corresponding orders.

spoken of as branches of the first order; those which, in turn, arise on branches of the first order as of the second order, and so on (cf. Fig. 82). The axis on which a daughter axis arises is termed relatively to it a parent axis. Parent axes may thus themselves be daughter axes of the first, second, third, etc., orders.

FIG. 83.—*Dictyota dichotoma*. (⅔ nat. size. After SCHENCK.)

Cymose branching, which will be described in connection with the cormus, also occurs in Thallophytes.

In contrast to the TRUE BRANCHING described above, what is known as FALSE BRANCHING is found in some low filamentous Algae and Bacteria. It comes about by the filament breaking into two portions, still, however, held together by the mucilaginous sheath; each new end arising by the rupture can grow on as a filament (Fig. 86). When an unbranched thallus is subsequently split into a number of lobes, as in the case of the flat thallus of *Laminaria* (Fig. 351), the term branching is not used.

The thallus in the **Fungi**, which do not assimilate carbon dioxide

but absorb organic substances, has a correspondingly peculiar aspect. It is termed a MYCELIUM, and consists of thin, highly-branched, cylindrical, colourless filaments (Fig. 87 and Fig. 6) called HYPHAE. These penetrate the substratum, such as the humus soil of a wood, in all directions and thus expose a large surface for the absorption of the necessary food materials. Parasitic fungi, if not inhabiting the cells, usually send suctorial projections of the hyphae (haustoria) into the living cells of the host plant from the hyphae in the intercellular spaces (Fig. 85).

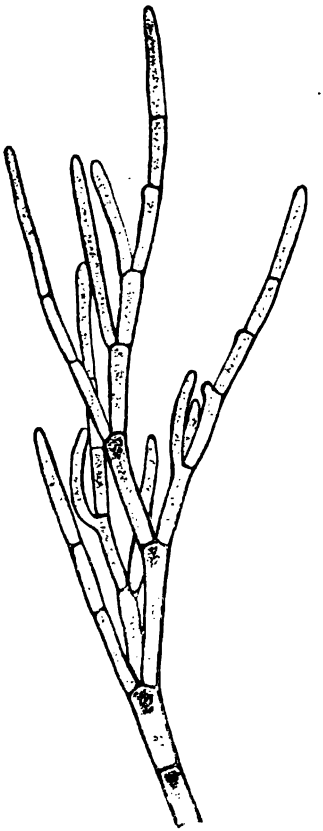


FIG. 84.—Portion of *Cladophora glomerata*. (× 48. After SCHENCK.)

7. Division of Labour between the Branches of the Thallus.—The most highly-segmented types of thallus are met with in some Siphoneae and in the Brown and Red Seaweeds (Phaeophyceae and Rhodophyceae). The external segmentation of some of these resembles in a remarkable manner the shoot in cormophytes. Some of these Algae attain a great size, the thallus

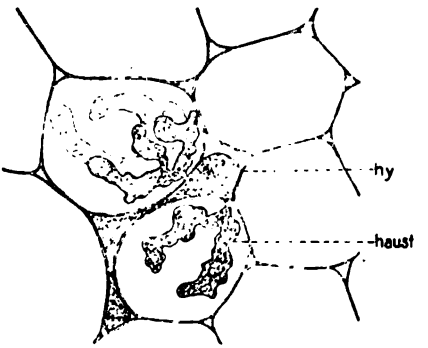


FIG. 85.—Haustoria (*haust*) of *Peronospora parasitica* in parenchymatous cells of *Capsella*. *hy*, The intercellular hyphae. (× 240.)

of the Brown Alga, *Macrocystis*, being 45 m. long. A good example of high differentiation is afforded by the Red Seaweed, *Delesseria sanguinea* (Fig. 88), which has leaf-like lateral branches seated on the cylindrical, branched, relatively main axes. In many such forms, besides the formation of attaching organs or haptera and of branches, a further degree of differentiation is attained. Some cylindrical branches continue the growth and branching of the thallus as LONG SHOOTS. Other branches borne on these are SHORT SHOOTS with

limited growth, and serve as leaf-like ORGANS OF ASSIMILATION. These short shoots may again exhibit a division of labour among themselves. Such forms are of the greatest interest morphologically, as they show how the leaves of cormophytes could have arisen from short shoots.

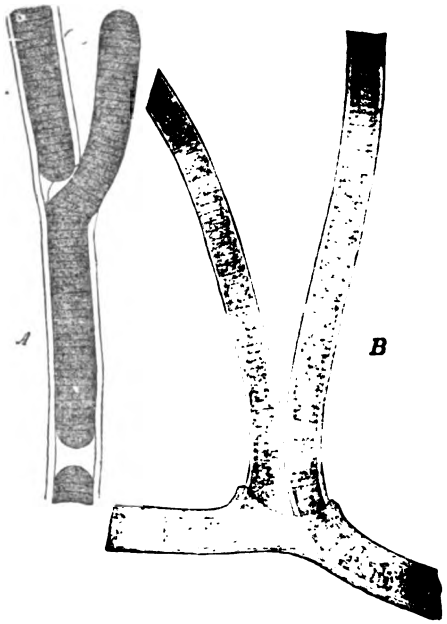


FIG. 86.—False branching in Cyanophyceae. *A*, *Plectonema Wollei*; only the upper end of the broken filament grows out as a branch. *B*, *Pl. mirabile*; both ends proceed to grow. (OLTMANNS after KIRCHNER and BORNET.)

Leaf-like short shoots have evidently arisen independently in a number of series of thalloid plants. These organs, serving for assimilation, have all assumed similar leaf-like forms. Thus the leaf-like branches of the Siphoneae and Brown Algae are not homologous with those of the Red Algae but only analogous.

8. Internal Structure of the Thallus. — Thalli, whether segmented or unsegmented, may consist of a single protoplast (*e.g.* Siphoneae, *Caulerpa*, Fig. 346) or of many cells. In the latter case the cells are arranged in filaments (Fig. 84), surfaces, or are united to form a cell mass. The simplest multicellular thalli are composed of uniform cells all capable of division. As soon as a growing point is defined a distinction between MERISTEMATIC and PERMANENT cells is apparent. The extreme tip of the apical growing point is nearly always occupied by a single cell termed the APICAL CELL. This often differs little from the other cells, as in the case of *Cladophora glomerata* (Fig. 84). The dome-shaped apical cell is prominent on the multicellular long shoots of the Brown Alga, *Cladostephus verticillatus* (Fig. 89).

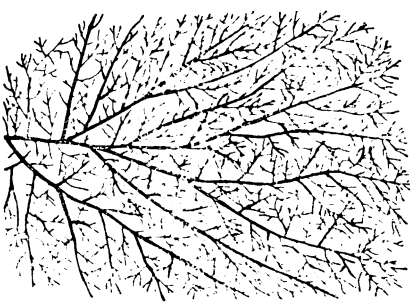


FIG. 87.—Portion of the mycelium of *Penicillium*. (× about 35.)

Such an apical cell divides by transverse walls parallel to one another, which cut off disc-shaped segments from its lower end. These divide further in a regular way, first by longitudinal and then by transverse walls into a number of cells, which are at first meristematic. The lateral branches, mostly developed as shoots of limited growth, develop from lateral cells in acropetal succession, and give the characteristic form to the plant (Fig. 89). Flat ribbon-shaped thalli may have a similar but correspondingly flattened apical cell, as seen in the Brown Seaweed, *Dictyota dichotoma* (⁵²) (Fig. 90). Flat segments are cut off from this by walls convex backwards, and are then divided by longitudinal walls. Sometimes the apical cell is divided by a longitudinal wall into two cells of equal size lying

FIG. 88.—*Delesseria sanguinea.* (½ nat. size. After SCHENCK.)

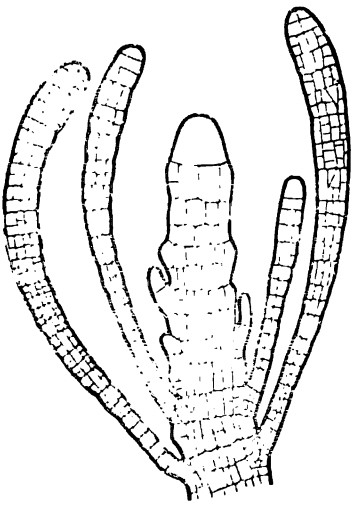


FIG. 89.—*Cladostephus verticillatus.* (× 80. After PRINGSHEIM.)

side by side (Fig. 90 *B*, *a*, *a*), each of which forms one of the branches of the dichotomy.

The permanent cells even of highly-differentiated thalli almost always have the characters of parenchyma. There may be a distinction of peripheral assimilatory parenchyma with abundant chlorophyll, storage parenchyma, colourless and with abundant reserve materials, and conducting parenchyma composed of elongated cells.

Since the multicellular Algae living in water do not require protection against drying up, and when exposed to the air at ebb-tide are protected by a covering of mucilage, a typical epidermal layer is wanting. The Algae show, however, an outer lamella of the cell walls of their superficial cells, which stains brown with

chlor-zinc-iodide. Rigidity of the thallus, especially in forms that grow exposed to the surf, is provided for by thickening of the walls of the outer layers of cells and sometimes by incrustation with calcium carbonate. In the Bladder Wrack (*Fucus vesiculosus*) special mechanical cells, characterised by their thickened walls and their great extensibility and elasticity, are present. The Laminarieae, which are also Brown Algae, attain the highest grade of internal differentiation. In the thick stem-like axis of these plants a cortex, a central body, and a loose medulla can be distinguished. The cortex frequently contains mucilage canals, and the medulla has rows of cells resembling sieve-tubes and serving for the transport of materials; such cells also occur in some Rhodophyceae. The axis grows in thickness by the continued division of a cortical layer, which forms concentric zones of secondary tissue, recalling the annual rings of the higher plants.

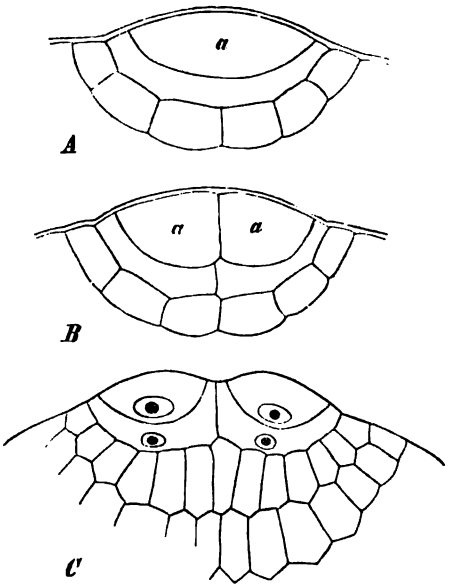


FIG. 90.—The growing point of *Dictyota dichotoma*, showing the dichotomous branching. *A*, Initial cell. (× circa 500. After E. DE WILDEMAN.)

The thalli of LICHENS arise by the interweaving of fungal hyphae and can assume a parenchymatous structure. The peripheral layers in many species form a protective rind owing to the close association of the hyphae and the thickening of their walls.

(b) Bryophyta[53].—The fact that the Mosses and Liverworts (Bryophyta) assimilate carbon dioxide finds expression in their external form and internal structure. There are Liverworts such as *Riccia fluitans* (Fig. 91) in which the dichotomously-branched ribbon-shaped body resembles the thallus of *Dictyota* (Fig. 83). In *Blasia pusilla*, another Liverwort (Fig. 92), the ribbon-shaped thallus has a midrib and bears lateral lobes as if the separation of leafy structures was commencing. The most completely segmented Liverworts, such as *Plagiochila asplenioides* (Fig. 93), and all the Mosses have cylindrical branched stems bearing such leaves as organs of assimilation. The lateral branches stand beneath the leaves on the main axis. These dorsiventral, bilateral, or radially-symmetrical bodies, which are often in the Mosses associated in tussocks, are only analogous to the shoots of the higher plants and are best regarded as highly-differentiated thalli. Though these plants, in contrast to the Algae, are mostly sub-aerial organisms they do not possess true roots, but are attached to the soil by RHIZOIDS. These are unicellular hairs, separated from the basal cell bearing them by a cross wall, or

branched filaments of cells, and serve to absorb water. Many of these plants can absorb water by their whole surface.

FIG. 91.—*Riccia fluitans.* (Nat. size. After SCHENCK.)

FIG. 92.—*Blasia pusilla.* *r*, rhizoid. (× 2. After SCHENCK.)

When the thallus lies on the substratum it is usually dorsiventral as in Lichens, and frequently has abundant chlorophyll only on the upper side exposed to the light (Fig. 95). In such cases the rhizoids are confined to the lower surface.

In the Bryophyta, which are all multicellular, the summit of the apical growing point is frequently occupied by a single apical cell.

In ribbon-shaped Liverworts, such as *Metzgeria* and *Aneura*, as in some similarly-shaped Algae, the apical cell is wedge-shaped (Fig. 94), and cuts off segments in two or sometimes four rows. The segments in the former case are cut off by oblique walls inclined alternately to the right and left; the four-sided apical cell in addition cuts off segments above and below. By further division the segments give rise to the body of the plant. The apparently dichotomous branching of Liverworts with growing points of this type can be traced back to the early delimitation of a new apical cell in the acroscopic half of a young segment (Fig. 94 at *b*). In the erect radially-constructed thalli of the Mosses the apical cell has the form of a three-sided pointed pyramid, and cuts off three rows of segments. The young leaves of the Mosses grow at first by a two-sided apical cell, but later have intercalary growth.

FIG. 93.—*Plagiochila asplenioides* with leaves overlapping like the laths of a Venetian blind. (Nat. size. After SCHENCK.)

The permanent tissues reach a higher level of differentiation than in the Algae. This is connected with the difficulties which the life on land of the Bryophyta introduces. There is only rarely a definite epidermis, though the superficial cells are covered by a kind of cuticle. On the thallus of the Marchantiaceae, however, an external layer of cells is clearly marked off from the underlying

tissue. It is perforated by air-pores (Fig. 95), which resemble in origin the stomata of higher plants. Hairs, in the form of mucilage-secreting papillae or flat leaf-like scales, are of common occurrence.

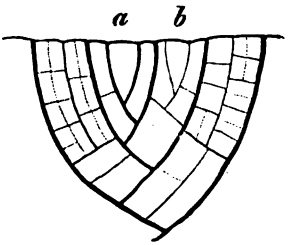


FIG. 94.—Diagrammatic representation of the apex of *Metzgeria furcata* in process of branching, viewed from the dorsal side. *a*, Apical cell of parent shoot; *b*, apical cell of daughter shoot. (× circa 370. After KNY.)

A typical stomatal apparatus with two guard cells enclosing a stoma is found, as GOEBEL (54) has shown in the thallus of the Liverwort, *Anthoceros*; it must be borne in mind that these stomata are mucilage slits and do not contain air.

A peculiar capillary apparatus serving for the absorption of water occurs in the Bog Mosses (Sphagnaceae). The cortex of the stem consists of three or four layers of empty cells, the walls of which have annular and spiral thickening, and are perforated by round holes; these readily absorb water. Similar cells lie singly in the leaves, which are only one layer of cells thick, in the meshes of a network of elongated living cells containing chlorophyll.

Some Liverworts have a strand of elongated cells serving for conduction. This is situated in the midrib of the ribbon-shaped forms. Conducting strands clearly limited from the surrounding tissue are, however, first met with in the Mosses.

A relatively simply-constructed conducting strand is shown in transverse section in the stem of *Mnium undulatum* in Fig. 96 *l*. The most perfect strands of this

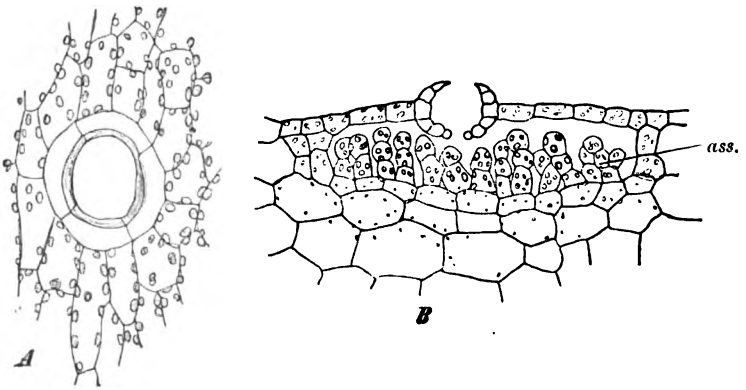


FIG. 95.—Surface view and transverse section of the thallus of *Marchantia polymorpha*. In *A*, an air-pore, as seen from above; in *B*, as seen in cross-section *ass*, assimilating cells. (× 240. After STRASBURGER.)

kind are found in the stems of the Polytrichaceae. They contain elongated, thin-walled, water-conducting elements, thick-walled mechanical tissue, and elongated cells that contain proteids and starch. Strands of similar construction are also found in the thick midrib of the leaves and are connected with that of the stem.

In some Mosses there are in addition elongated and pointed mechanical cells which closely resemble sclerenchyma fibres.

(c) Gametophyte of the Cormophytes ([53]). In the developmental history of the cormophytes a stage with a thalloid vegetative body occurs. Two generations alternate regularly with one another, the spore-bearing plant or sporophyte and the sexual plant or gametophyte. The vegetative body of the former is a cormus, while that of the latter is usually a very simply segmented and constructed thallus (prothallium). In Pteridophyta the gametophyte is usually a flat green structure attached to the soil by rhizoids and living independently (Fig. 97). It is at most a few centimetres in length and resembles a small Liverwort thallus. It may also consist of branched filaments.

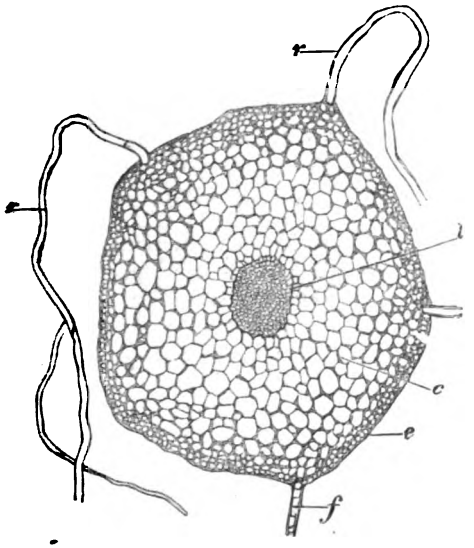


FIG. 96.—Transverse section of the stem of *Mnium undulatum*. *l*, Conducting-bundle; *c*, cortex; *e*, peripheral cell layer of cortex; *f*, part of leaf; *r*, rhizoids. (× 90. After STRASBURGER.)

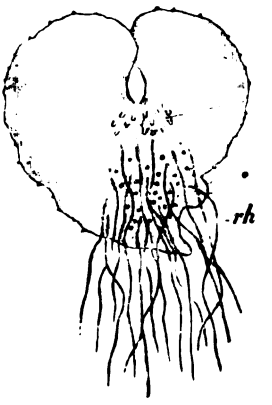


FIG. 97.—*Aspidium filix mas*. Prothallium from the lower side. *rh*, rhizoids. (× about 8. After SCHENCK.)

B. THE CORMUS

The vegetative organs of the sporophyte in the Ferns and fern-like plants (Pteridophyta) and in the Spermatophyta, to which the name cormus will be applied, are, as has already been mentioned, more highly segmented than the thalli. The cormus is divided into shoot and root, the shoot into the axis and the leaves. Stems, leaves, and roots are thus the fundamental organs of the cormus, which evidently is adapted to life on land by its outer and inner construction.

As in many thalli the surface of the cormus is considerably increased by branching. The shoot forms lateral branches, the roots give rise to lateral roots, and by this branching, which in many plants begins even in the embryo, a shoot-system and root-system arise.

The term cormus is usually employed as equivalent to shoot to denote a leafy stem apart from the roots, and a shoot or cormus is then recognised in the leafy Bryophyta. This view, however, dates from a period when the life-history of the Bryophyta was not accurately known. It is now established that the "shoot" of the Moss is not homologous with the shoot of the higher plants. It is therefore advisable not to employ the terms shoot or cormus in speaking either of the Bryophyta or of similarly organised Algae. There is nothing to prevent using the conception of the cormus as a wider one than that of the shoot, and to understand by it the vegetative organs of the cormophytes differentiated into shoots and roots. Further, there are transition forms between roots and shoots (*e.g.* the rhizophores of *Selaginella*) and between leaves and shoots (*e.g. Utricularia*).

1. Construction of the Typical Cormus

The fundamental organs of those cormi which can be regarded as typical will be considered in the first place. Their peculiarities only appear typically in such plants as our native trees, or even more clearly in many herbs. The fundamental organs may undergo many modifications and, in extreme cases, their distinction may be difficult.

(a) The Shoot

The shoot in land plants may be wholly or in part exposed to the air (AERIAL SHOOT) or be partly buried in the soil (SUBTERRANEAN SHOOT, Fig. 138); the latter is the case in many perennial herbaceous plants (cf. Figs. 123, 138). It consists of the STEM or AXIS of the shoot and the LEAVES. The latter on the aerial shoots, which are usually green, are developed as foliage leaves, while on the white or colourless subterranean shoots (root-stocks or RHIZOMES) they are mere scales. The stem bears the leaves and provides for the extension of the shoot-systems; this involves the elongation of the stem and the formation of new leaves and lateral branches, the connection between the leaves and roots, and the conduction of material between these organs. The stem in most subterranean shoots further serves as a place of storage of reserve materials. The foliage leaves, like the leaf-like branches of thalloid plants, are the organs of assimilation and transpiration in the cormophytes. The external form and internal structure of the foliage leaves and stem stand in relation to these functions.

(α) **The Growing Point.**—The shoot grows by means of an apical growing point situated at the extreme tip of the stem. Since the growing point is extremely small and scarcely visible to the naked eye, it is best seen when longitudinal sections of the apex of the shoot

are examined with a magnifying glass (Fig. 98). It then appears flat (Fig. 99) or convex (Fig. 98 *v*), and sometimes distinctly conical (Figs. 100, 102). The rudiments of the leaves (*f*) and of lateral branches (*g*) arise laterally beneath the tip and appear as closely-crowded exogenous projections or bulges of the surface. The leaves arise in acropetal order and become larger on passing farther from the apex, as is clearly shown in transverse sections of the growing point (Fig. 99).

The growing point and the young leaves, which only arise from the embryonic part of the apex, both consist of meristematic tissue. In the majority of the Ferns and in the Horsetails a single apical cell

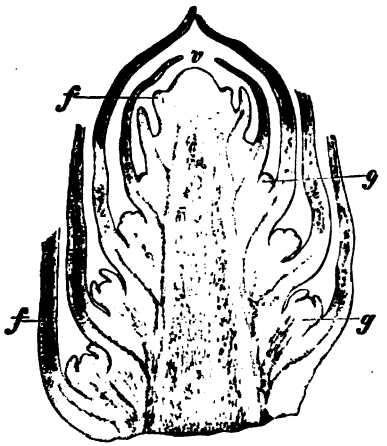


FIG. 98.—Apex of a shoot of a phanerogamic plant. *v*, Vegetative cone; *f*, leaf-rudiment; *g*, rudiment of an axillary bud. (× 40. After STRASBURGER.)

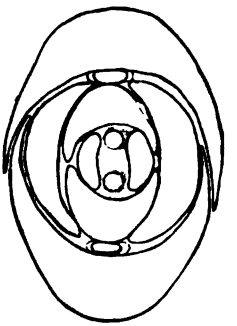


FIG. 99.—Apical view of the vegetative cone of a shoot of *Euonymus japonica*. (× 12. After STRASBURGER.)

is found at the summit of the growing point (Fig. 100 *t*). It has the form of a three-sided pyramid (tetrahedron) with a convex base.

The apical cell (Fig. 100 *t*, 101 *A*) of the main shoot of the Common Horsetail (*Equisetum arvense*) will serve as an example. Viewed from above (Fig. 101 *A*) it appears as an equilateral triangle in which new walls are successively formed parallel to the original walls. Each segment (*S'*, *S''*) becomes further divided by partition walls. In the Pteridophyta which have apical cells the leaf rudiments (*f*, *f'*, *f''*) usually commence their development with an apical cell which cuts off the rows of segments (*f*). The activity of this usually ceases, and the development of the leaf is continued by marginal growth due to a number of equivalent two-sided cells. This is the case, for example, in *Equisetum*. The lateral buds (*g*) also start from a single cell that becomes the apical cell.

In the Lycopodiaceae, among the Pteridophyta, and in Phanerogams, there is no such single apical cell at the growing point. In

place of this a number of equivalent meristematic cells, which often form regular concentric layers (Fig. 102), are met with.

The outermost layer of cells which covers the growing point and also the developing leaves is termed the DERMATOGEN (*d*) because it gives rise to the epidermis; it usually divides by anticlinal walls only. The cells in which the central cylinder of the stem ends at the apex form the PLEROME (*pl*), while the layers between this and the dermatogen constitute the PERIBLEM (*pr*). The limit between the periblem and plerome is often indistinct. The leaves and lateral branches arise as multicellular projections (Fig. 102), which come about by local increase in number of periblem cells, while the dermatogen undergoes anticlinal divisions only

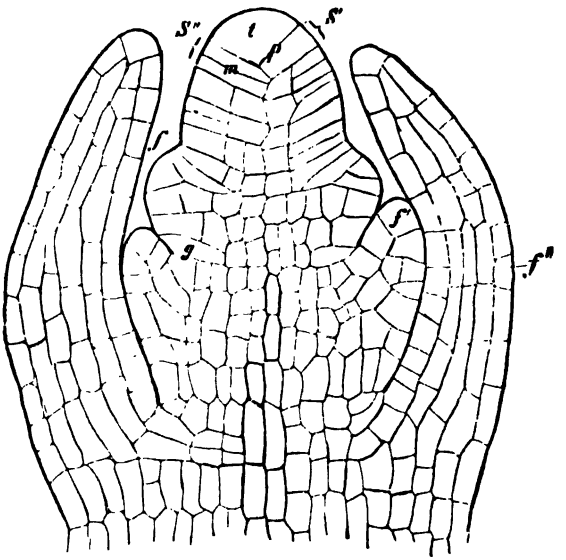


FIG. 100.—Median longitudinal section of the vegetative cone of *Equisetum arvense*. Explanation in the text. (× 240. After STRASBURGER.)

and keeps pace with the enlargement. In the case of the origin of leaves only the dermatogen and periblem are concerned; in that of the lateral branches the plerome also (55).

Since the rule that the new cell walls intersect at right angles holds for growing points, the system of cell walls as seen in longitudinal sections often forms a strikingly symmetrical figure, the periclinal as well as the anticlinal walls forming systems of confocal parabolas (Fig. 266). The elements of the one system cut those of the other nearly at right angles (SACHS). In transverse sections of such growing points the periclinal walls form concentric circles.

BUD.—The formation of new members at the growing point is followed by their increase in size and differentiation. This applies in the first place to the young leaves, the growth of which exceeds that of the stem apex and is most marked on their lower surfaces. As a

result of this the older leaves close over the growing point (Fig. 98) and the younger leaf rudiments. The growing point thus becomes a bud in which the delicate younger structures are protected against desiccation by the older and larger, though still immature, leaves. A bud is thus the young incompletely-developed end of a shoot.

VERNATION AND AESTIVATION.*—A section through a winter bud shows a wonderful adaptation of the young leaves to the narrow space in which they are confined. They may be so disposed that the separate leaves are spread out flat, but more frequently they are folded, rolled (Fig. 103 *l*), or crumpled. The manner

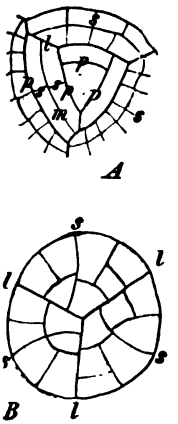


FIG. 101.—*A*, Apical view of the vegetative cone of *Equisetum arvense*. *B*, Optical section of the same, just below the apical cell; *l*, lateral walls of the segments. Further explanation in text. (× 240. After STRASBURGER.)

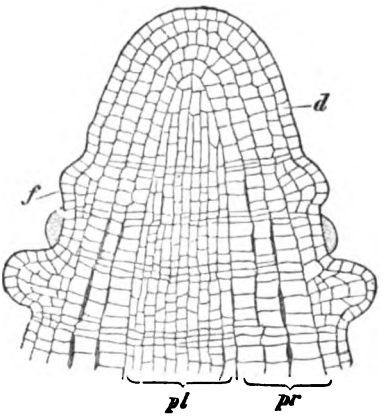


FIG. 102.—Median longitudinal section of the vegetative cone of *Hippuris vulgaris*. *d*, Dermatogen; *pr*, periblem; *pl*, plerome; *f*, leaf-rudiment. (× 240. After STRASBURGER.)

in which each separate leaf is disposed in the bud is termed VERNATION. On the other hand, the arrangement of the leaves in the bud with respect to one another is designated AESTIVATION. In this respect the leaves are distinguished as FREE when they do not touch, or VALVATE when merely touching, or IMBRICATED, in which case some of the leaves are overlapped by others (Fig. 103 *k*). If, as frequently occurs in flower-buds, the margins of the floral leaves successively overlap each other in one direction, the aestivation is said to be CONTORTED.

(β) The Axis of the Shoot. A. External Construction.—The active elongation of the stem begins at some distance from the growing point; with this the leaves in the bud begin to separate. It is characteristic of shoots, especially aerial shoots, that this elongation is not limited to a short region below the bud but extends many centi-

* [The use of these terms in the following paragraph differs from that customary in England. By VERNATION is understood the arrangement of the leaves in a vegetative bud as a whole. The folding of each individual leaf in the bud is termed PTYXIS. The term AESTIVATION is applied to the arrangement of the parts in a flower-bud.—TRANS.]

metres (to more than 50 cm.) from this. It is not of course so active in the successively distant zones. The elongation may, on the other hand, be so slight that the mature leaves of the shoot adjoin one another without leaving any free surface of stem between them. As a rule, however, its amount and distribution is such that the insertions of the leaves become separated by bare regions of stem (Fig. 115). These are known as INTERNODES, while the transverse zones of the stem where the leaves are inserted are the NODES. The growth in length is much less in the nodes than in the internodes. In the latter it is often limited to a narrow zone, for example at the base of the internode in the Grasses. There are then a number of zones of intercalary growth in the stem separated by fully-grown regions. The nodes may be swollen (cf. Labiatae).

FIG. 103.—Transverse section of a bud of *Populus nigra*. *k*, Bud-scales showing imbricated aestivation [vernation]; *l*, foliage leaves with involute vernation [ptyxis]; *s*, each leaf has two stipules. (× 15. After STRASBURGER.)

In the aerial shoots the internodes are usually thin, while they are frequently very thick in subterranean shoots.

The length of successive internodes of an axis exhibits a certain regularity. Usually it increases on ascending a main axis and then diminishes.

Leaf Arrangement ([56]).—The distribution or arrangement of the leaves is very characteristic of shoots, and exhibits great variety. One or a number of leaves may be borne at each node. When there are several leaves they form a WHORL and are termed the members of the whorl, while the leaf arrangement is spoken of as VERTICILLATE. When there is only one leaf at each node the arrangement is ALTERNATE. A very remarkable and peculiar regularity is exhibited by the arrangement of leaves on all sides of erect shoots; it is often at once evident when the growing point is looked at from above (Figs. 99, 104). The youngest leaf-rudiments adjoin the older ones in such a way as to best utilise the available space. The relations of position are best shown when they are plotted diagrammatically on a ground-plan. The position of the leaves is represented in the diagram, which is of a plane at right angles to the axis of the stem, as if the latter were conical and viewed from the tip; it is thus possible to indicate a higher position on the stem by a more internal position in the plan. Such ground-plans of leaf arrangements are called DIAGRAMS (Fig. 105). The centre corresponds to the apex of the stem; the leaves nearest to this are the youngest or uppermost, and those

farther out are successively older and lower. It is convenient to indicate each node by a circle; when there are several leaves at the same node they are represented on the same circle. Such diagrams agree with the figures of transverse sections of a bud in the neighbourhood of the apex of the stem (Figs. 99, 104).

It thus appears that EVEN AT THEIR APPEARANCE THE LEAVES ON AN ERECT RADIAL SHOOT ARE DISPOSED AS REGULARLY AS POSSIBLE AROUND THE STEM. THIS ENSURES THAT THE EXPANDED LEAVES DO NOT SHADE ONE ANOTHER BUT MAKE THE FULLEST POSSIBLE USE OF THE LIGHT. The distribution is so regular that the angle between two successive leaves (*e.g.* in Fig. 105, leaves 1 and 2, 2 and 3, etc.) is constant; this is termed the ANGLE OF DIVERGENCE, or, when

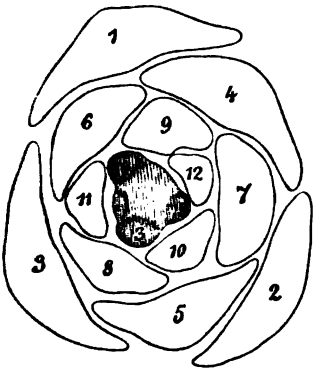


FIG. 104.—Transverse section of a leaf-bud of *Tsuga canadensis*, just below the apex of the shoot, showing a $\frac{2}{5}$ divergence. (× circa 20. After HOFMEISTER.)

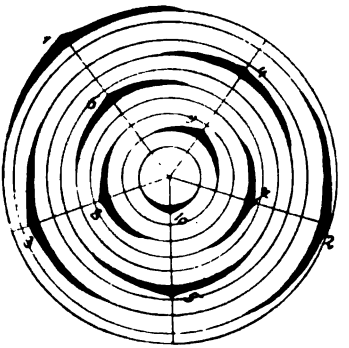


FIG. 105.—Diagram showing $\frac{2}{5}$ position of leaves. The leaves numbered according to their genetic sequence. (After STRASBURGER.)

expressed as a fraction of the circumference, the DIVERGENCE. It is different in different kinds of plants.

In the case of verticillately-arranged leaves the angle of divergence of a whorl (Fig. 106) is the circumference divided by the number of leaves, which is usually the same in each whorl. The members of successive whorls do not stand immediately above one another but alternate, so that the members of one whorl come above the intervals between those of the whorl below (Fig. 99, 106). The result of this arrangement, combined with the equality of the angle of divergence in each whorl, is that the leaves of such a shoot are arranged in twice as many vertical rows as there are members in each whorl (Fig. 106). These longitudinal or vertical ranks are termed ORTHOSTICHIES. A frequent case of verticillate arrangement is that of whorls of two members (Figs. 99, 106). In this arrangement, which is termed DECUSSATE, the angle of divergence is 180°; the divergence is thus $\frac{1}{2}$, and there are four orthostichies. If there are three members in a whorl the angle of divergence is 120°, the divergence $\frac{1}{3}$, and there are six orthostichies.

When the arrangement of the leaves is alternate the divergence may be $\frac{1}{2}$ (Fig. 107), $\frac{1}{3}$ (Fig. 144), $\frac{2}{5}$ (Fig. 105), $\frac{5}{13}$ (Fig. 104), etc. Here also, owing to the uniformity of the angle of divergence, the leaves will stand in orthostichies on the stem. With a divergence of $\frac{1}{3}$ leaf 4 will stand vertically over leaf 1 (5 over 2, 6 over 3, 7 over 1, etc.); with a $\frac{2}{5}$ divergence (Fig. 105) leaf 6 comes over leaf 1, 7 over 2, 8 over 3, etc. If one imagines the insertions of successive leaves connected by the shortest line passing round the circumference of the stem, this line will be a spiral. The alternate arrangement of leaves is therefore also spoken of as SPIRAL ARRANGEMENT. The segment of this genetic spiral passing from leaf to leaf till one vertically over the starting point is reached is called a CYCLE of the spiral (*e.g.* in Fig. 105 from 1-6 or 3-8). In the case of $\frac{1}{2}$ divergence the cycle consists of three leaves and passes once round the stem. In $\frac{2}{5}$ divergence (Fig. 105) the cycle consists of five leaves and passes twice round the stem. In the fraction expressing a divergence the numerator shows how often the cycle passes round the stem, and the denominator how many leaves the cycle includes. The latter also indicates how many orthostichies there are and which leaf will next be found in the same orthostichy. For example, in a $\frac{5}{13}$

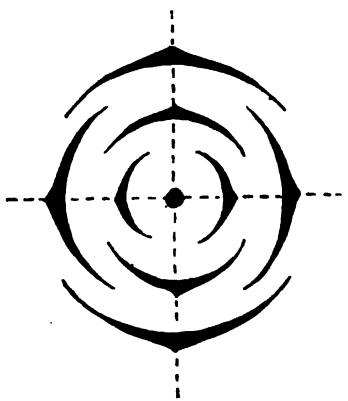


FIG. 106.—Diagram of the decussate arrangement of leaves. The dotted lines are the orthostichies. (Modified after STRASBURGER.)

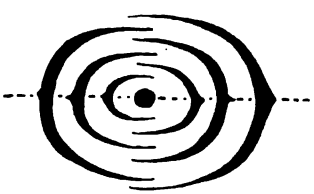


FIG. 107.—Diagram of two-ranked arrangement of leaves. The dotted lines are the orthostichies. (Modified after STRASBURGER.)

divergence the stem will be passed round five times before the next superposed leaf is met with, there are 13 orthostichies, leaf 16 stands over leaf 3 (3 + 13), and over leaf 8, leaf 21 (8 + 13). Since the denominator always indicates the number of orthostichies, the $\frac{1}{2}$ divergence is also spoken of as two-ranked, the $\frac{1}{3}$ divergence as three-ranked, etc. When the leaves on a stem are crowded and in contact another series of ascending spirals becomes more prominent; these are the PARASTICHIES. They come about by the contact of those leaves the lateral distance between which on the axis is the least. The parastichies appear very clearly on pine-cones from which Fig. 108 is prepared as a somewhat diagrammatic view from the base. In this view the parastichies appear as spiral lines. Several systems of parastichies running in the same direction are clearly apparent. One of these (indicated by the unbroken lines I-VIII) goes in the direction of the hands of a clock; two cross this system, one being a flat and the other a steep spiral, and these are marked by the two types of dotted lines. Two systems of equivalent parastichies that cross can be used to determine the divergence (cf. Fig. 108). Denoting any particular leaf by 1, the number of the next leaf in the parastichy is obtained by adding to 1 the number of the oblique ranks of that system which pass round the stem. There are 8

parastichies indicated by unbroken lines, so that the next leaf in this parastichy is 1+8=9 and the next to this 9+8=17, etc. Taking the opposite system of spirals there are 5 marked by broken lines (13 marked by dotted lines), and thus the leaves in the system with broken lines are 1+5=6, 6+5=11, and so on. In the dotted parastichies, on the other hand, they are 1+13=14, 14+13=27, etc. This regularity depends on the fact that in every system of parastichies there must be as many leaves between the successive leaves of one parastichy as the remainder of the parastichies of that system. (This, in the system indicated by unbroken lines in Fig. 108, is 7, and seven leaves intervene between 1 and the next leaf of the parastichy. This leaf must follow on 1+7 and therefore be number 9.) If all the leaves are numbered in this way the successive numbers 1, 2, 3, 4, etc., give the genetic spiral and the divergence. The pine-cone in Fig. 108 has the leaf arrangement $\frac{5}{21}$, and in accordance with this the leaves 1, 22, 43 come above one another—*i.e.* in the same orthostichy. When the divergences are determined in diverse plants with alternately-arranged leaves it is found that certain divergences are particularly common. The series $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, $\frac{8}{21}$, $\frac{13}{34}$, etc., can thus be arrived at. These fractions have an evident connection with one another; the numerator and denominator of each are the sums of the numerators and denominators respectively of the two preceding fractions. The divergences of this series all lie between $\frac{1}{2}$ and $\frac{1}{3}$ of the circumference of the stem. They deviate the less from one another as the start of the series is departed from and approach more and more an angle of 137° 30′ 28″. This series is termed the main series of leaf arrangements. There are also other similar series, but the main series is characterised by the fact that by its divergences the most uniform spacing of the leaves on an axis is attained with the smallest number of leaves. The discoverers of this series were CARL SCHIMPER and ALEXANDER BRAUN.

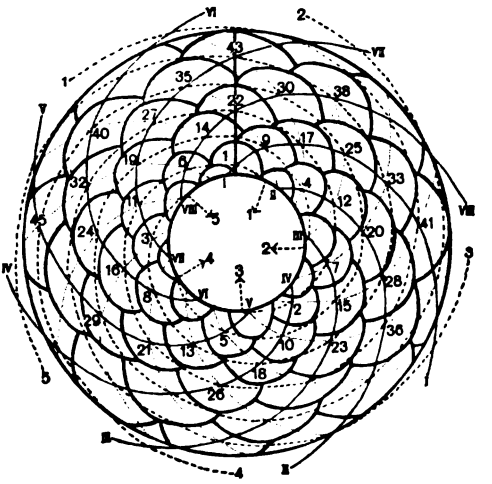


FIG. 108.—Semi-diagrammatic view of a pine-cone seen from below. Divergence of scales $\frac{5}{21}$; I-VIII, system of parastichies running in the direction of the hands of a watch; 1-5, system of parastichies running in the opposite direction. For further description see the text.

Erect radial shoots with elongated internodes or with broad leaves have usually few orthostichies, while those with short internodes and narrow leaves have many. In the latter case the divergences belong to the higher members of the series.

Changes in the original position of the leaves may be caused by torsions of the axis. Thus the leaves at the growing point in species of *Pandanus* are laid down in three vertical series, but subsequently come to be arranged by the torsion of the stem in three spiral lines. In this way the leaves can better utilise the light.

The arrangement of the leaves on inclined dorsiventral stems is relatively simple. A divergence of $\frac{1}{2}$ or a similar arrangement is the most common; by this

the leaf surfaces can be placed horizontally and obtain favourable illumination. This is frequently attained by twisting of the internodes, which thus transforms a decussate into a two-rowed arrangement on inclined shoots. Similar changes occur in the case of alternately-arranged leaves in relation to the best utilisation of the light by the leaf surfaces. The position of the foliage leaves is nearly always an adaptation to the needs of the plant as regards light. In some horizontal subterranean shoots (*e.g.* of Ferns) the leaves stand in one row on the upper side.

Practically nothing is known of the causes of the regularity in the arrangement of leaves. The assumption of SCHWENDENER that purely mechanical causes acting at the places of origin of the leaves determined the arrangement of the latter has proved to be unfounded [57]. The leaves need not arise at the apex in the order of their genetic spiral, nor simultaneously as members of a whorl. Sometimes one side of a growing point may even predominate in the production of leaf-rudiments.

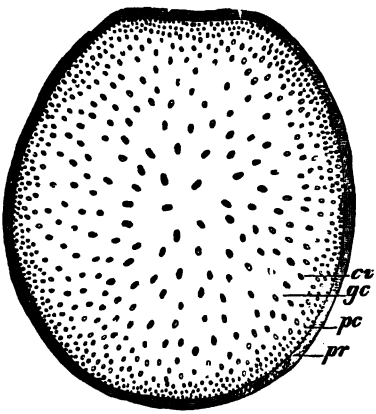


FIG. 109.—Transverse section of an internode of the stem of *Zea Mais*. *pr*, Primary cortex; *pc*, pericycle; *cv*, vascular bundles; *gc*, fundamental tissue of the central cylinder. (× 2. After SCHENCK.)

B. Primary Internal Structure of the Stem [58].—The stem exhibits a much more advanced differentiation of tissues than the long shoots of even the most highly segmented thalli. On the outside a typical EPIDERMIS forms its boundary layer. Beneath this in the internodes (the nodes have a more complicated structure to be considered later) comes a zone of tissue free from vascular bundles and called the CORTEX. This surrounds the CENTRAL CYLINDER (Fig. 109), as the remaining tissue of the stem including the vascular bundles is called.

It is practically desirable to maintain the conception of a central cylinder even though in some Monocotyledons the cortex cannot be clearly distinguished from the central cylinder and the vascular bundles occur close below the epidermis.

Cortex.—The cortex is mainly composed of parenchyma. In green aerial shoots the peripheral layers contain chlorophyll, while those farther in are colourless and serve for storage rather than assimilation. In colourless subterranean stems, which often attain a greater thickness, it is composed of colourless parenchyma which, like the parenchyma of other regions of the rhizome, contains reserve materials. Mechanical tissue is also developed in the cortex. The stem in aerial shoots sustains the weight of the leaves and is exposed to bending by the wind; it must be sufficiently rigid against bending in all directions. This is attained by the aid of mechanical tissue as

layers or strands of collenchyma or sclerenchyma; this is placed as near to the periphery as possible, sometimes lying just below the epidermis of projecting ridges (Fig. 111, 1, 2).

RIGIDITY AGAINST BENDING while the least possible mechanical material is employed is best attained by placing this in a peripheral position. When a straight rod (Fig. 110) is bent the convex side elongates and the concave side is shortened. The outer edges, *a*, *a* and *a'*, *a'*, are thus exposed to the greatest variations in length, while nearer the centre (*i*, *i*; *i'*, *i'*) the deflection and consequent variations in length are less. If instead of the uniform rod the mechanically effective material were disposed as economically as possible, it should be brought close to the periphery. In this position it will oppose the greatest resistance to bending, and if bending takes place will be less easily torn or crushed than less resistant material. Every one knows how great is the resistance to bending of an iron tube, even with thin walls. The builder attains a high level of resistance to

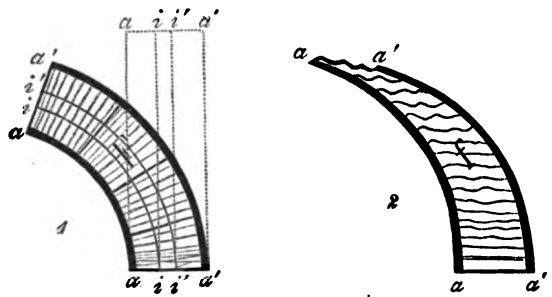


FIG. 110.—1. Longitudinal section of an elastic cylinder, before bending (dotted outline) and after bending (heavy outline). After bending the convex side (*a'*) is stretched and the concave side (*a*) compressed. *f*, Connecting tissue.

2. When the connecting tissue (*f*) is not sufficiently firm, the bands of stereome (*a*, *a'*) curve independently and remain unaltered in length. (After NOLL.)

bending by placing at the periphery of structures bars of mechanically effective material parallel to one another and to the longitudinal axis of the structure. These are called girders. It is essential that these GIRDERS should be connected and kept at their proper distances from one another by a sufficiently rigid but elastic connecting tissue (Fig. 111, 1). Each rod or girder then forms with the one lying immediately opposite an I-girder, the material which occupies the line between the two rods being the connecting material (Fig. 110). Were this connection wanting each rod would be readily bent. In hollow structures, however, it is sufficient that the girders should be joined laterally. In large buildings the peripherally-placed bars have themselves the construction of I-girders, each being constructed of two connected bars.

As SCHWENDENER (44) first showed, the mechanical tissues which render a stem rigid against bending are arranged so as to make the best use of the material. In many plants the mechanical tissue forms a peripheral hollow cylinder which may either come next the epidermis or be more deeply situated (Fig. 112 *pc*); in others there is a system of similarly-placed strands of mechanical tissue lying side by side (system of simple girders, Fig. 111, 1); the latter arrangement may be combined with the complete hollow cylinder (Fig. 111, 2). In other cases each of

the peripheral strands has itself the form of an I-girder (Fig. 111, 3); only the outer bars of this consist of mechanical tissue, the connection being usually made by a vascular bundle (system of compound I-girders). These arrangements are on the whole better shown in the stems of Monocotyledons than in the primary structure of the stems of Dicotyledons and Gymnosperms. In the latter the rigidity can be increased by the secondary thickening. In stems which are green and carry on assimilation the mechanical tissue is somewhat removed from the epidermis, being separated from the surface by the green tissue for the functions of which light is necessary; in other cases the mechanical and assimilatory tissues share between them the peripheral position (Fig. 111, 2).

The innermost layer of cells of the cortex in the mature subaerial stems of land plants is not usually specially characterised. There is

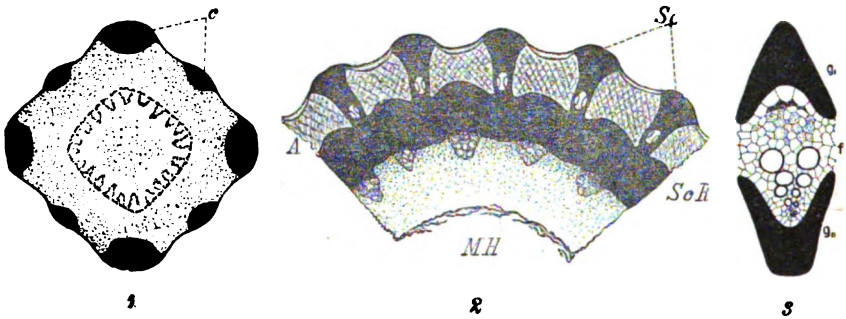


FIG. 111.—Rigidity against bending. 1. Transverse section of a young twig of *Sambucus*; *c*, collenchyma. 2. Part of the transverse section of a haulm of grass (*Molinia coerulea*); *Sc*, ribs of sclerenchyma; *Sc R*, sclerenchymatous ring connecting them laterally; *A*, green assimilatory tissue; *MH*, pith-cavity. 3. Diagram of double girder on a larger scale. *g*, *g*, Girders; *f*, connecting tissue represented by the vascular bundle. (1 and 2 after NOLL.)

then no sharp limit between cortex and central cylinder. This layer may, however, be developed as a starch sheath, as a typical endodermis (especially in the subterranean shoots of land plants and in the stems of aquatic plants), or as a cutis. If developed as a STARCH SHEATH (*st*, Fig. 112 *A*, *B*) its cells contain large, easily-movable starch grains.

The starch sheath is often present in the young shoots only and disappears or remains limited to certain spots in the older condition. In place of a common starch sheath or endodermis such sheaths may be found around the separate bundles (Fig. 119 *pp*), or there may be single rows of cells containing easily-movable starch.

Central Cylinder.—This is composed of various tissues. The parenchyma, in accordance with its deep-seated position, is almost or quite colourless, and serves mainly for conduction or storage. Sclerenchyma frequently is present. The most important parts of the central cylinder are, however, the VASCULAR BUNDLES which serve for the carriage of water with the necessary salts from the roots to

the leaves, and on the other hand conduct organic substances from the leaves to the root system. The bundles are embedded in the other tissues of the central cylinder and contrast with these owing to the narrowness of their elements and the absence of intercellular spaces. When the central cylinder and cortex are sharply delimited by a sheath the vascular bundles do not as a rule abut on this, but are separated by a zone one or more layers thick (Fig. 112 *A*, *B*, *pc*) which is called the PERICYCLE.

The vascular bundles have a definite course and consequently a special arrangement as seen in a transverse section of the stem. In transverse sections of the internodes they appear arranged in a circle

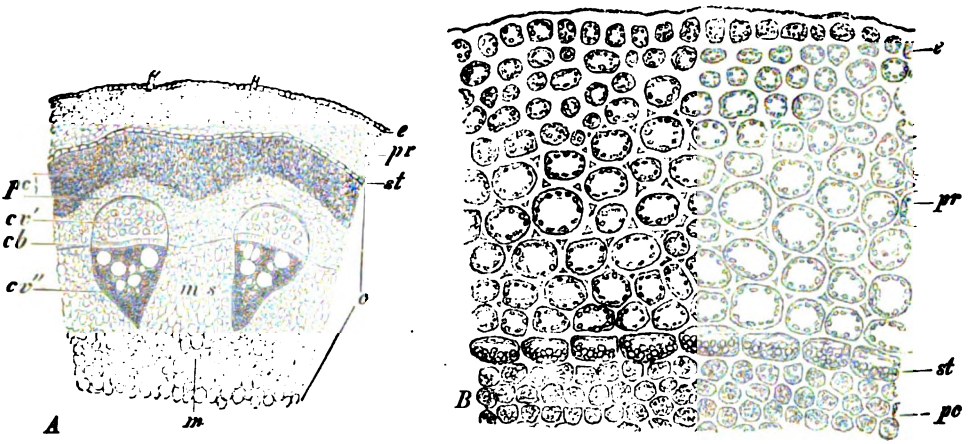


FIG. 112.—*A*, Part of transverse section of a young stem of *Aristolochia Sipho*. *e*, Epidermis; *pr*, primary cortex; *st*, starch sheath; *c*, central cylinder; *pc*, pericycle, in this case with a ring of sclerenchyma fibres; *cv'*, phloem, and *cv''*, xylem portions of the vascular bundle; *cb*, cambium ring; *m*, medulla; *ms*, primary medullary ray. (× 48.) *B*, Small portion of the periphery of a similar section of a still younger stem. *e*, Epidermis; *pr*, primary cortex; *st*, starch sheath with easily-movable starch grains; *pc*, outer layers of the pericycle. (× 350. After STRASBURGER.)

in the Horsetails (*Equisetum*) and most Gymnosperms and Dicotylédons (Fig. 111,'1). In most Ferns and in Monocotyledons (Fig. 109), on the other hand, they are irregularly scattered. If the bundles form a single circle (Fig. 112 *A*) the tissue within this, composed of parenchymatous cells which are alive or may die at an early period, is distinguished as the PITH (*m*). The tissue between the bundles forms the MEDULLARY RAYS (*ms*). This distinction is wanting when the bundles are scattered (Fig. 109).

There are also Dicotyledons in which the vascular bundles form two (*Cucurbita*, *Phytolacca*, *Piper*) or more circles (*Amarantus*, *Papaver*, *Thalictrum*). The more internal circles are usually less regular.

The medullary rays may consist of parenchyma, but in a number of herbs their

inner portion, between the xylem of adjacent bundles, is formed of sclerenchyma. This contrasts with the outer parenchymatous portions situated in the region of the phloem.

Subterranean shoots and submerged plants which have to withstand pulling forces have their mechanical tissue more or less centrally placed; it may be in the pith.

Course of the Vascular Bundles.—In accordance with their functions the vascular bundles form continuous strands which in macerated preparations may be followed from the root-tips to the extremity of the leaves. This can be done by letting herbaceous plants lie in water until all the tissues except the more resistant vascular bundles have decayed and disappeared.

The bundle of the root is traced to the base of the shoot, where it is continuous with the more complicated system of vascular bundles (cf. p. 137). The bundles in the stem may be traceable to the apex without passing into the leaves. Such bundles are termed CAULINE, and contrast with purely FOLIAR bundles which immediately on entering from a leaf unite with cauline bundles.

Thus in the Pteridophyta there may be a network of cauline bundles or a single central bundle (*Lycopodium*, etc.) with which the foliar bundles unite on entering from a leaf-base.

As a rule, however, the bundles of the shoot bend outwards into leaves and are COMMON bundles, the upper portion of which belongs to a leaf and the lower portion to the stem. One or several such bundles pass into a leaf and form collectively what is known as the leaf-trace. The vascular system of the stem in the seed plants consists as a rule entirely of these leaf-traces or common bundles.

The stems of some Dicotyledons (*Begonia*, *Aralia*) possess cauline bundles in the pith enclosed by the circle of common bundles. At the nodes these cauline bundles, which may be arranged in a ring concentric with the common bundles, are connected with the latter.

The leaf-trace bundles may remain separate from one another in the stem, but usually each descending bundle of the trace ends by joining another bundle that has entered from a lower leaf. A splitting or forking of the bundle may precede this junction. Such a reticulate arrangement of the bundles ensures a uniform distribution of the water supply, since each bundle of the stem as a consequence of its subdivision provides water to a larger region of the shoot. The general course of the bundles differs in different species according to the length of the free course of the single bundles of the trace, the course they follow, and the subdivision they undergo. The arrangement of the leaves naturally determines the places of entry of the leaf-traces into the stem. Their course in the stem is, however, quite independent of the leaf arrangement, and can be very different for one and the same type of this.

In the Horsetails, the Coniferae, and the Dicotyledons, all the leaf-trace strands penetrate equally deeply into the stem to pass down this as parts of the characteristic ring of bundles evident in transverse sections. The course of the bundles in the internode can thus be indicated on the surface of a cylinder or represented as if this surface were flattened in one plane. Complications occur at the nodes by the leaf-trace strands being joined by transversely-placed cauline strands; cross connections of later development often occur in the internodes also.

A relatively simple example of the arrangement of vascular bundles is afforded by the young shoots of *Juniperus nana* (Fig. 113), the leaves on which are in whorls of three. From each leaf a leaf-trace consisting of a single vascular bundle enters the stem. This divides into

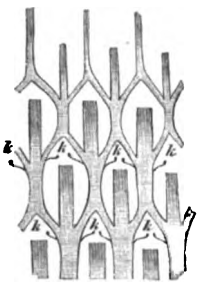


FIG. 113.—Diagram of the course of the vascular bundles in a young branch of *Juniperus nana* shown on the unrolled surface of the cylinder. At *k*, *k* the vascular bundles passing to the axillary shoots are seen. (After GEYLER.)

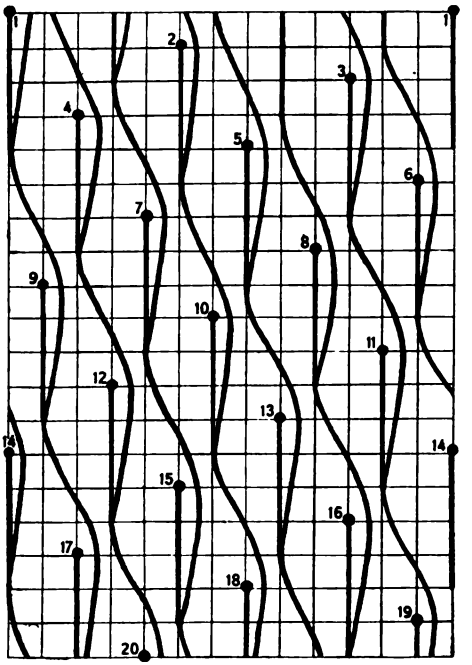


FIG. 114.—Diagrammatic representation of the course of the vascular bundles in a young twig of *Taxus baccata*. The tube of bundles is slit up at 1, and spread out in one plane.

two about the middle of the internode below, and the portions diverge right and left to unite with the adjacent leaf-traces. The arrangement of the bundles in a young twig of *Taxus baccata* as shown in Fig. 114 is less simple, though in this case also the leaf-trace consists of only one bundle. Each leaf-trace can be followed down through twelve internodes before it joins on to another bundle. It first runs straight down for four internodes and then bends aside to give place to an entering trace, with which it later unites. In *Taxus* the leaf insertions, and consequently the places of entry of leaf-traces, have a divergence of $\frac{5}{12}$. An example of leaf-traces composed of three bundles is afforded by young branches of *Clematis viticella*, the arrangement of the leaves on which is decussate. The median strands of the leaf-traces (*a* and *d*, *g* and *k*, *n* and *q*, *t* and *x* in Fig. 115) run down through one internode, dividing at the next done into two arms which fuse with the adjacent lateral strands of the leaves

inserted at this node. The two lateral strands of each leaf-trace (Fig. 115 *b, c*; *e, f*; *h, i*; *l, m*; *o, p*; *r, s*) are also free through the internode, but at the node below they curve inwards and become attached to the same lateral strands as the arms of the median bundle of the trace.

The course of the bundles in the Monocotyledons follows a wholly different type (Fig. 116). The individual bundles of the leaf-trace penetrate to different depths in the stem and thus appear scattered on the cross-section. This results from the prolonged growth in thickness of the growing point after the procambial strand of the first and median bundle of the leaf is laid down. As a result of this the successively-formed procambial strands of the later bundles are placed less deeply. This arrangement is especially well marked in the Palms (palm type), in which each leaf-trace consists of the numerous bundles which pass into the stem from the leaf-base which completely encircles the stem. The median bundle penetrates to the centre of the stem, the lateral bundles, as the median line of the

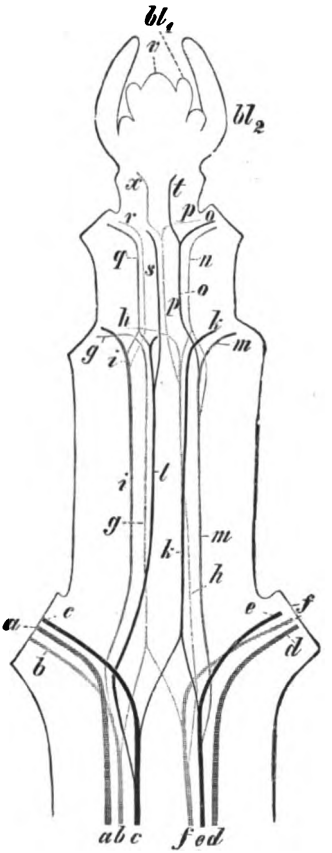


FIG. 115.—*Clematis viticella*. End of a branch which has been made transparent by the removal of the superficial tissues and treatment with caustic potash. The emerging strands have been slightly displaced by gentle pressure. The two uppermost pairs of young leaves (*bl* 1, *bl* 2) are still without leaf-traces. *v*, Apical cone. (After NÄGELI.)

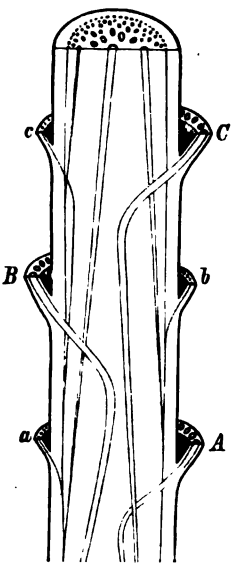


FIG. 116.—Diagrammatic representation of the course of the bundles in the Palm type. Two-ranked leaves encircling the stem are shown cut in their median planes. The leaves (*Aa*, *Bb*, *Cc*) are cut across close to the base; the capital letters indicate the median portion of each. The stem is seen above in transverse section. (After ROTHERT, adapted from ROSTAFINSKI.)

leaf is departed from, less and less deeply. In the longitudinal section of a stem in Fig. 116 only the median bundle for each leaf (*A*, *B*, *C*) and one lateral bundle (*a*, *b*, *c*) are represented. In their further downward course the bundles gradually approach the periphery of the stem, where they fuse with others. The number of internodes which each bundle traverses varies, being greatest for the median bundle.

Structure of the Vascular Bundles (59).—The bundles in the stem are strands of tissue of circular or elliptical outline in cross-section and always consist of xylem and phloem, *i.e.* are complete bundles (cf. p. 67). The sieve-tubes are the most important component of the phloem portion and the water-conducting vessels of the xylem portion of the bundle. The bundles are variously constructed in different cormophytes, all the types being represented in the stem (radial, concentric, and collateral bundles). These types are distinguished from one another by the arrangement of the strands of xylem and phloem.

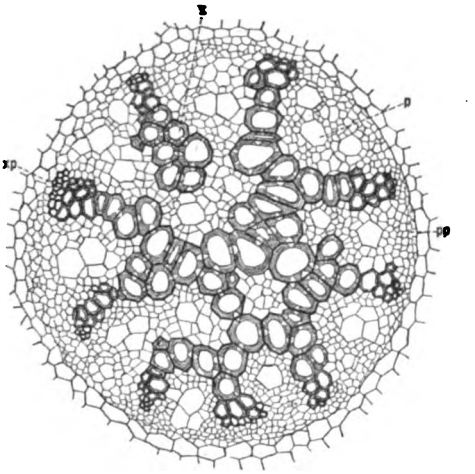


FIG. 117.—Radial vascular bundle from the stem of *Lycopodium Hippuris*. *p*, Phloem; *pp*, primary phloem; *x*, xylem; *xp*, protoxylem. (× 30.)

In RADIAL vascular bundles (Fig. 117; cf. also Figs. 161, 163) there are a number of strands of xylem and phloem which, as seen in a cross-section of the circular bundle, stand side by side, alternating with one another. Seen from the side the vascular strands run parallel to one another and to the longitudinal axis of the part of the plant. The strands of xylem may meet in the centre of the bundle and so constitute a star-shaped mass as seen in transverse section. The ends of the rays are made up of the narrowest tracheides (protoxylem), while the vessels towards the centre are always wider (Fig. 117). The strands of phloem are situated in the depressions between the rays, the narrow protophloem elements being at the periphery. Radial bundles, though characteristic of roots, occur relatively seldom in stems and are always solitary, as for example in the stems of *Lycopodium*.

In CONCENTRIC bundles a central strand of xylem or phloem is surrounded on all sides by a cylinder of phloem or xylem. The bundle may be distinguished as concentric with internal xylem when the xylem is centrally placed, and as concentric with outer xylem

when this tissue is peripheral. The bundles in most Pteridophytes (Fig. 119) are of the former type, those in the rhizomes or stems of some Monocotyledons (Fig. 118) of the latter.

In the Pteridophytes the narrow elements of the protoxylem (*sp*) lie in groups in the strand of xylem, peripherally, centrally, or among the later-formed vessels. The xylem is surrounded by a sheath of parenchyma (*lp*). Outside this comes a zone composed of sieve-tubes (*v*) and parenchyma (*s*), the narrow protophloem elements being situated at the outer edge of this.

In COLLATERAL vascular bundles (Fig. 120 *A*), which consist of a strand of xylem and as a rule a single strand of phloem, the xylem lies beside or rather behind the phloem. The median plane of the bundle is always placed radially in the stem, the xylem being directed inwards and the phloem outwards. The protoxylem in collateral bundles is usually placed at the inner edge of the strand of xylem, the protophloem at the outer edge of the phloem, as the bundle is seen in transverse section. Such collateral bundles are characteristic of the shoots of the Spermaphyta and the Horsetails. BICOLLATERAL bundles, in which the xylem is accompanied by a strand of phloem on the inside as well as on the outside, also occurs, as for example in the stems of Cucurbitaceae. In Monocotyledons the collateral bundles, like the radial and concentric vascular bundles, are closed, *i.e.* the whole bundle consists of permanent tissue, the xylem abutting directly on the phloem (Fig. 120 *A*). In Gymnosperms and Dicotyledons, on the other hand, the bundles are usually open, *i.e.* the xylem and phloem remain separated by a layer of meristematic tissue called the CAMBIUM (Fig. 121).

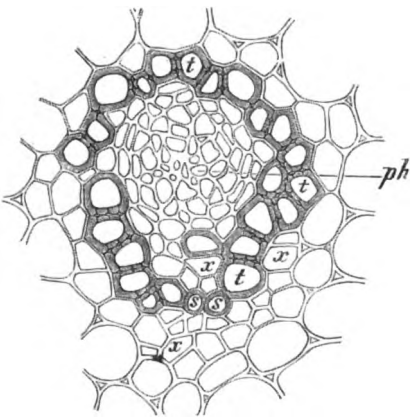


FIG. 118.—Concentric vascular bundle with external xylem from the rhizome of *Convallaria majalis*. *ph*, Phloem; *x*, *t*, xylem; *s*, protoxylem. (After ROTHERT.)

In all vascular bundles the strands of xylem are mainly composed of narrower or wider lignified elements that serve for the conduction of water. These may be tracheides and tracheae, or only tracheides. They occur singly or in groups without intercellular spaces among narrow, living, elongated and often unlignified cells of the conducting parenchyma (xylem parenchyma), or are surrounded by a sheath of this tissue (Fig. 119 *lp*). Sclerenchymatous fibres are sometimes present in addition. In the Pteridophyta only tracheides are present, while in the bundles of Phanerogams both tracheae and tracheides

usually occur. In all bundles the narrowest vessels are annular or spiral; the others are usually reticulated or pitted, but in the Pteridophyta the elements, apart from the protoxylem, are scalariform (Fig. 70 *A*).

In the strands of phloem of the vascular bundles (Figs. 119, 120) the sieve-tubes (*v*) which serve for the conduction of proteids are always accompanied by other living cells. These are either the

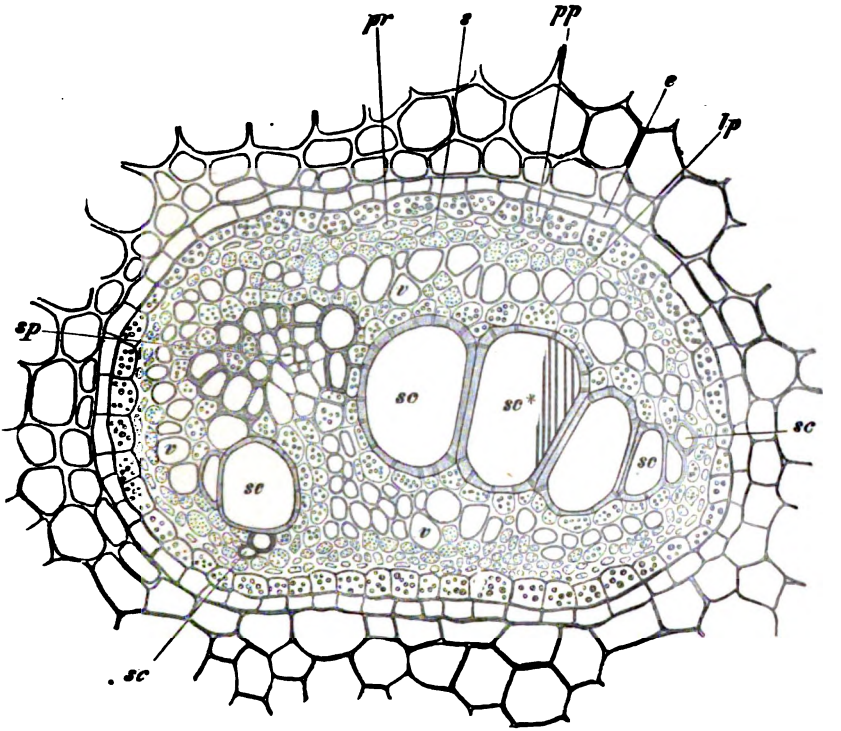


FIG. 119.—Transverse section of a concentric bundle from the petiole of *Pteris aquilina*. *sc*, scalariform vessels; *sp*, protoxylem (spiral tracheides); *sc**, part of a transverse wall showing scalariform perforations; *lp*, xylem parenchyma; *v*, sieve-tubes; *pr*, protophloem; *pp*, starch layer; *e*, endodermis; *s*, phloem parenchyma. (× 240. After STRASBURGER.)

COMPANION CELLS (Fig. 120 *s*), which are usually shorter than the elements of the sieve-tubes with which they connect by sieve-pits, companion cells together with other elongated parenchymatous cells (phloem parenchyma), or PHLOEM PARENCHYMA only (Fig. 119 *s*). When the latter tissue is present the sieve-tubes are embedded in it singly or in groups without intercellular spaces.

Companion cells only occur in relation to the sieve-tubes of Angiosperms. They are sister cells to the members of the sieve-tube, cut off by a longitudinal

division, and later undergoing as a rule transverse divisions. They are narrower than the sieve-tubes themselves, and are further distinguished from them by their abundant protoplasmic contents. In some cases laticiferous- or mucilage-tubes occur in the phloem.

The bundle as a whole is often more or less completely surrounded by a BUNDLE SHEATH. This may have the form of parenchyma without intercellular spaces, the cells often containing large starch grains

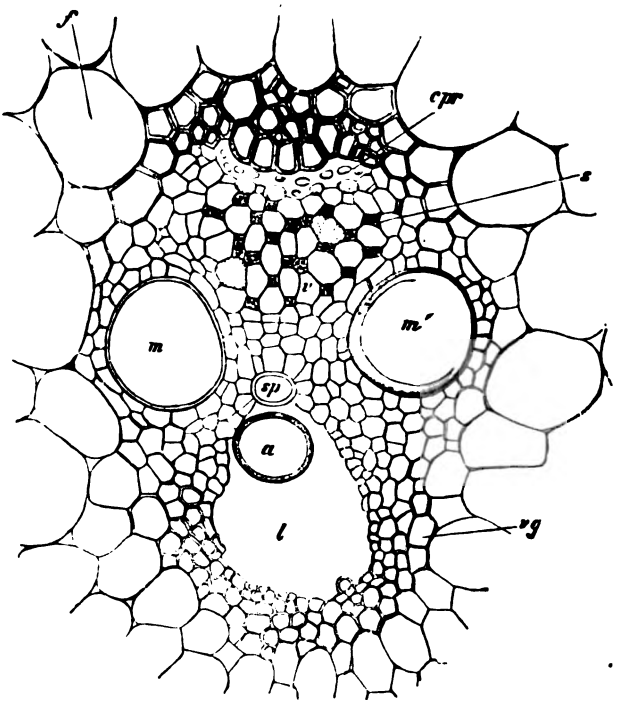


FIG. 120 *A*.—Transverse section of a vascular bundle from the internode of a stem of *Zea Mais*. *a*, Ring of an annular tracheide; *sp*, spiral tracheide; *m* and *m'*, vessels with bordered pits; *v*, sieve-tubes; *s*, companion cells; *cpr*, compressed protophloem; *l*, intercellular passage; *vg*, sheath; *f*, cell of fundamental tissue. (× 180. After STRASBURGER.)

(STARCH SHEATH); in other cases it is sclerenchymatous, or it consists of endodermal cells or of cutis tissue. It is not regarded as forming part of the vascular bundle itself. The sheaths frequently serve to limit the conduction of material to the vascular bundle. Sclerenchymatous sheaths are most common at the outer side of the phloem, forming semilunar masses (Fig. 120 *A*, 121 *vg*), and are especially developed in relation to the outermost bundles when these have a scattered arrangement.

When a sclerenchymatous sheath surrounds a collateral bundle it is frequently interrupted at the sides, opposite the junction of the xylem and phloem, by parenchymatous or less thickened and lignified elements. These long strips facilitate the exchange of water and nutritive substances between the bundle and the surrounding tissues.

In order to understand the construction of the vascular bundles and the differences between the various types their ontogenetic development must be taken into consideration. The primary vascular bundles are developed from strands of elongated meristematic cells.

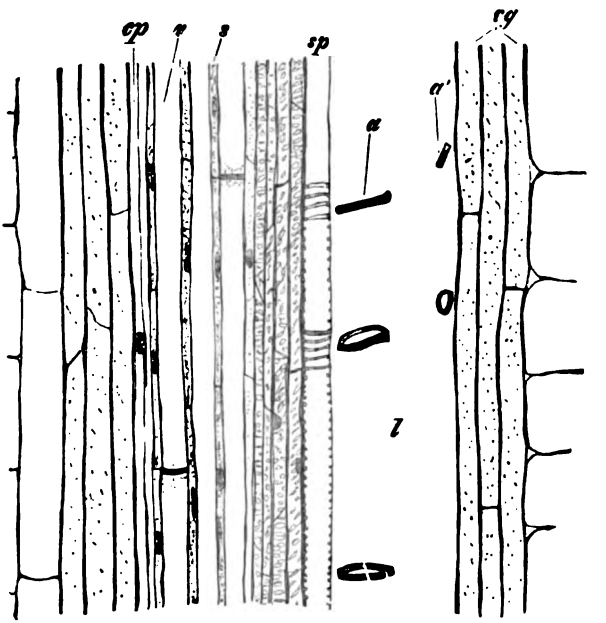


FIG. 120 *B*.—Longitudinal section of a vascular bundle from the stem of *Zea Mais*. *a* and *a'*, Rings of an annular tracheide; *v*, sieve-tubes; *s*, companion cells; *cp*, protophloem; *l*, intercellular passage; *vg*, sheath; *sp*, spiral tracheides. (× 180. After STRASBURGER.)

In these the differentiation of the tissues proceeds gradually over a period of time. So long as the portion of the plant is still growing actively in length the main portion of the strand of meristem remains undifferentiated. Only at limited regions of the strand, usually at the outer and inner margins, are a few elements transformed into permanent tissue. These elements, which are suited to undergo stretching, are on the one hand annular and spiral tracheides, and on the other sieve-tubes with or without companion cells. They form the protoxylem and protophloem respectively. Only when growth in length is finished do the bundles become fully differentiated, the differentiation proceeding from the protoxylem and protophloem. In

the xylem there is a succession of annular, spiral, reticulate, and finally pitted vessels (Fig. 120 *B*). The first-formed elements of xylem and phloem have ceased to be functional in the fully-developed vascular bundle. The protoxylem elements are then frequently compressed or torn by the stretching (Fig. 120 *l*, at *a*, *a'*), and in some cases their place is taken by a lysigenous intercellular space (Fig. 120 *l*). The

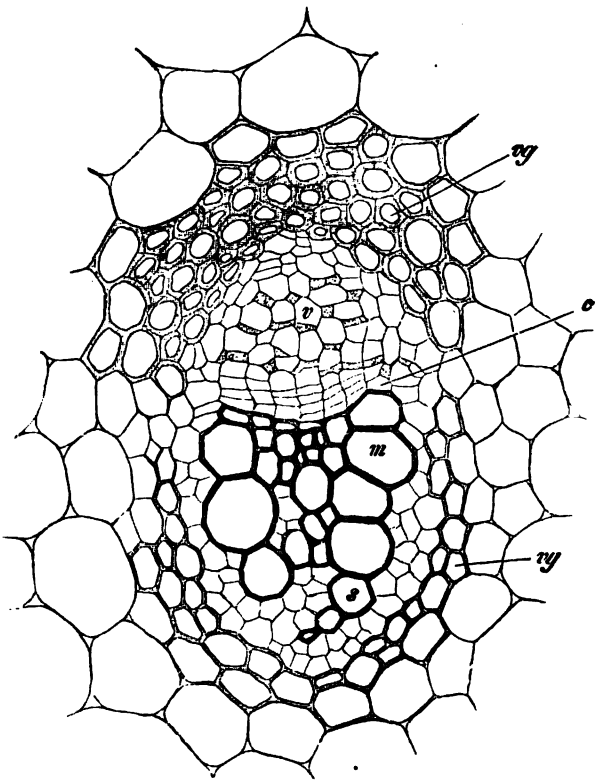


FIG. 121.—Transverse section of an open collateral vascular bundle from a stolon of *Ranunculus repens*. *s*, Spiral tracheides; *m*, vessel with bordered pits; *c*, cambium; *v*, sieve-tubes; *vg*, sheath. (× 180. After STRASBURGER.)

walls of the protophloem elements (*cp*) are swollen and their sieve-plates closed by callus.

In radial bundles the differentiation proceeds, in accordance with the position of the first formed elements in the strands of xylem and phloem, from the periphery towards the centre. In collateral bundles, on the other hand, the elements are developed in succession from the protophloem on the outside and the protoxylem on the inside towards

the middle of the bundle. If the meristem is completely used up in this process a closed collateral bundle results; if some remains between the xylem and phloem the bundle is an open one. In concentric bundles the development does not follow a single type, and in accordance with this the position of the protoxylem and protophloem is various.

Bundles in which the protoxylem is situated at the inner margin of the xylem (in collateral bundles) or in the centre, as is often the case in concentric bundles, are termed endarch. When the protoxylem elements are at the outer margin of the xylem, as in radial bundles, it is spoken of as exarch. When the protoxylem is in one or more groups removed both from the inner and outer margin of the xylem it is mesarch, *e.g.* in the petiolar bundles of the Cycadeae or in concentric bundles; the protoxylem in this case is embedded among the wider vessels.

It is not at present known what relation holds between the arrangement of xylem and phloem and the requirements of conduction in the plant, and whether any one of the three types of bundle, *e.g.* the collateral, is superior in this respect ([58], [59]).

The phylogeny of the types of bundle is also not clear. All the evidence points to the assumption that a stem with a single central vascular bundle is relatively primitive. Such a bundle is found in the stems of a number of living and extinct Pteridophyta and in all roots. The simplest and phylogenetically oldest type of vascular bundle appears to be the concentric bundle with a solid central strand of xylem; at least this appears to be present in the young plants of nearly all existing Ferns. The radial bundle also may be a very ancient type, as is suggested by its constancy in the roots of all living and extinct cormophytes so far as our knowledge extends and in the stems of some cormophytes. No other type of bundle is found in both stems and roots. The variety as regards the construction and arrangement of the bundles, which is met with in the shoots of Pteridophyta as contrasted with the Spermatophyta, leads to speculations upon the mode of origin of these various types of construction from stems with a single concentric bundle. There are stems in which the vascular tissue of the single central bundle has the form of a hollow cylinder enclosing a central strand of parenchyma or pith (Gleicheniaceae, Schizaeaceae). In others the hollow cylinder of xylem is lined with an internal zone of phloem (*e.g. Marsilia*). Lastly, there are cases in which the hollow vascular cylinder is perforated by rhombic leaf-gaps at the departure of the leaf-trace bundles (*e.g. Aspidium filix mas*). In this last case a cross-section of the stem shows a number of typically constructed concentric bundles, with solid central strands of xylem, arranged in a circle. There are also forms in which a cylinder of xylem immediately surrounding the pith is divided by radial plates of parenchyma into a number of longitudinally-running strands of xylem placed side by side, the whole being surrounded by a continuous zone of phloem (*e.g. Osmunda*). Lastly, there are cases in which the phloem is correspondingly divided so that the radial plates of parenchyma separate, as medullary rays, the collateral strands composed of xylem and phloem (*e.g.* rhizome of *Ophioglossum*). These examples show how either a reticulate tube of concentric bundles or a hollow tube composed of collateral bundles can be derived from a centrally-placed concentric bundle. If we assume that the phylogenetic development has proceeded on these lines, it is clear that neither one collateral bundle of the Spermatophyta nor one of the circle of concentric bundles found in many Ferns is homologous with the central bundle of "primitively constructed" Pteridophyta. The totality of collateral or

concentric bundles in such stems would be homologous with the single central concentric or radial bundle. According to this assumption, which is the essential of the STELAR THEORY (60), the single central bundle is termed the stele, and the circle of collateral or concentric bundles with the enclosed pith would also be regarded as a stele since it is derived from the primitive stele. A single bundle may therefore represent the whole stele or a part of the stele. There is usually only one stele or central cylinder in the stem of the Spermatophyta (monostely). Cases are, however, met with when the stele is divided (polystely) as in the stems of *Auricula* or *Gunnera*.

(γ) The Leaves. 1. Development of the Leaves.—The leaves

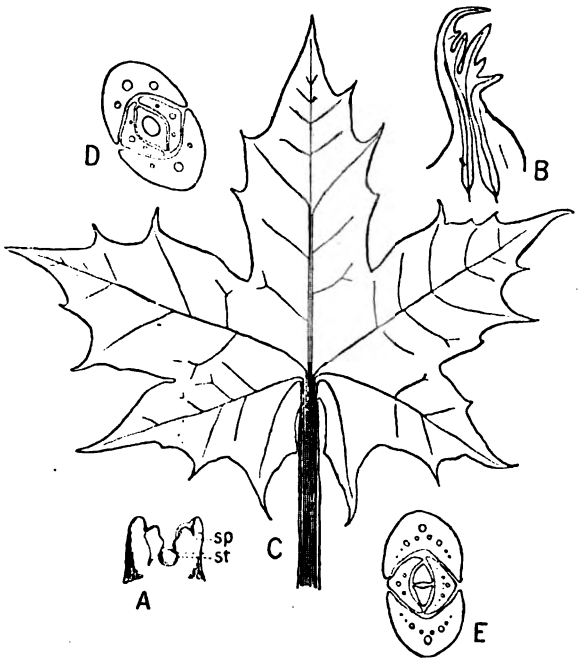


FIG. 122.—*Acer platanoides*. *A*, External view of a bud, with two young leaves between which the apical cone of the stem is visible; *sp*, the leaf-blade, in which five segments are indicated, the uppermost one being developed first; *st*, the zone, by the growth of which the leaf-stalk will arise later. *B*, An older leaf seen from the side; the young vascular bundles, which will later determine the venation, are indicated. *C*, Fully-grown leaf, with the course of the vascular bundles indicated diagrammatically. *D*, A transverse section of the basal portion of a bud showing three vascular bundles in each leaf. *E*, A similar section at a higher level; the number of vascular bundles has increased by branching. (After DEINEGA, from GOEBEL'S *Organography*. *A*, *B*, and *E* slightly magnified.)

have been seen to arise exogenously at the growing point of the stem as lateral papillae or bulges (Fig. 98, 102 *f*), which to begin with are unsegmented. These are the LEAF PRIMORDIA (Fig. 125 *A*, *b*). Usually a young leaf occupies only a part of the circumference of the apex, but it may encircle the latter as an annular ridge. Several

leaves forming a whorl may arise in the same way and only later appear as distinct structures on the ring-shaped outgrowth. When whorled leaves arise independently they may either appear simultaneously or, as is more commonly the case, in succession ([58, 59]).

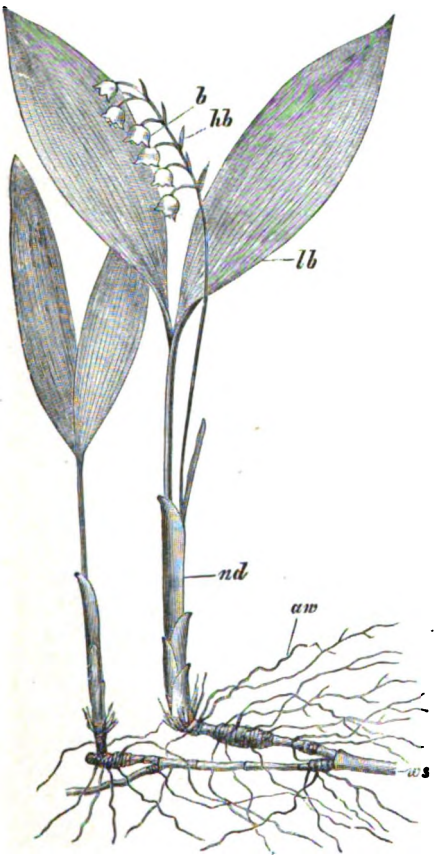


FIG. 123.—Lily of the Valley (*Convallaria majalis*). *nd*, Scale leaves; *lb*, foliage leaves; *hb*, bracts; *b*, flower; *ws*, rhizome; *aw*, adventitious roots. (Somewhat reduced. After STRASBURGER.)

In rare cases a leaf may be terminal on the growing point.

While the shoot by means of its growing point has an unlimited growth, the growth of the leaf primordia, which only continues at their tips for a short time, is limited. The tip, which often develops more rapidly than the rest of

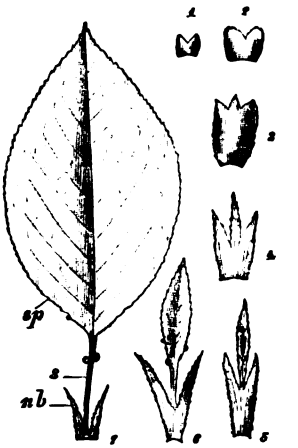


FIG. 124.—Bird Cherry (*Prunus avium*). Bud-scales (1-3) and the transition forms (4-6) to the foliage leaf (7); *sp*, leaf-blade; *s*, leaf-stalk; *nb*, stipules. (Reduced slightly. After SCHENCK.)

the leaf, is first transformed into permanent tissue. This assists in the protection of the youngest parts of the bud, a function which has already been seen to be undertaken by the leaves. The further growth of the leaf is as a rule effected by intercalary growth. Most frequently the change into permanent tissue proceeds from the tip towards the base. The growth is thus greatest and most prolonged in the leaf-base, where it continues until the leaf is fully developed.

The more rapid development of the leaf-tip is most striking in some tropical plants, especially in climbers. In this case, according to M. RACIBORSKI, these "fore-runner tips" perform the functions of the leaves before the remainder of the leaf has attained the mature condition.

Well-marked and long-continued apical growth is found in the leaves of some Ferns.

Welwitschia mirabilis behaves in a peculiar way unlike all other cormophytes. Above the cotyledons only a single pair of foliage leaves is formed. The basal zones of these grow in each annual period while the ends of the leaves are gradually withering.

2. Different Forms of Leaves.—The leaves of the shoot have very diverse functions and are correspondingly various in their form on the same stem, although in their origin they are alike.

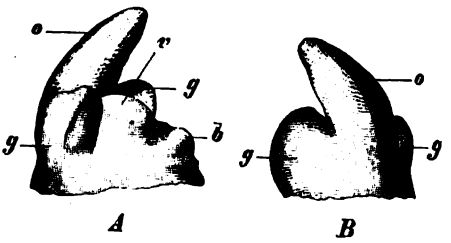


FIG. 125.—Development of the leaf in the Elm, *Ulmus campestris*. *A*, Showing the vegetative cone, *v*, with the rudiments of a young leaf, *b*, still unsegmented, and of the next older leaf, exhibiting segmentation into the laminar rudiment, *o*, and leaf-base, *g*. *B*, Showing the older leaf, viewed obliquely from behind. (× 58. After STRASBURGER.)

The main axis of the seedling bears first the COTYLEDONS or seed-leaves which are situated on the hypocotyl (Fig. 158) of the embryo while it is yet in the seed. In the Monocotyledons there is only one such leaf, while the Dicotyledons and some Gymnosperms have two cotyledons and some Gymnosperms have more than two. Following on the cotyledons in the case of subterranean stems, and often also in those above ground, come a number of SCALE LEAVES (Fig. 123 *nd*), then in the case of aerial shoots the FOLIAGE LEAVES (*lb*), and still higher simply formed BRACTEAL LEAVES (*hb*). The foliage leaves may be first considered since the other forms have arisen by transformation of these.

A. The Foliage Leaves exhibit a great variety of form and segmentation, and these characters are largely employed in descriptive botany. They may be simple as in the needles of Coniferae; in this case the primordial leaf has only to increase in size and lengthen. As a rule, however, the foliage leaf is segmented into the flattened, thin, bright-green LEAF-BLADE (lamina, Fig. 124 *sp*), which is often inaccurately spoken of as the leaf; the stem-like LEAF-STALK (petiole, Fig. 124 *s*); and frequently also into the STIPULES (*nb*) attached to the LEAF-BASE close to the stem or into a LEAF-SHEATH (vagina, Fig. 133 *v*) more or less completely surrounding the stem above the node. When the leaf-stalk is wanting the leaf is termed sessile; when present it is petiolate. The segmentation is recognisable at an early stage in the primordial leaves, which are differentiated shortly after

their origin into the leaf-base (Fig. 125 *A* and *B*, *g*) and the upper leaf (Fig. 125 *A*, *B*, *o*). From the leaf-base the stipules (*g*) arise or it forms a leaf-sheath or a thickened pulvinus. Frequently it undergoes no special further development and is not distinguishable in the mature leaf. The leaf-blade (Fig. 116 *A*, *sp*) is developed from the upper leaf, and so also when this is present is the leaf-stalk (*A*, *st*). The latter develops relatively late by intercalary growth and is thus intercalated between the already present leaf-blade and leaf-base; it is never inserted directly on the stem.

(a) The Leaf-blade. External Form (Fig. 127).—The leaf-blade,

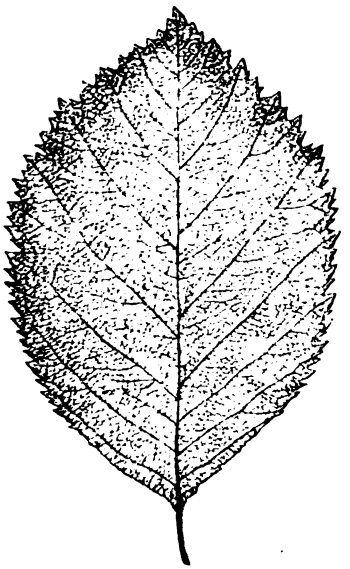


FIG. 126.—Leaf of *Crataegus* with reticulate venation. (⅓ nat. size. After NOLL.)

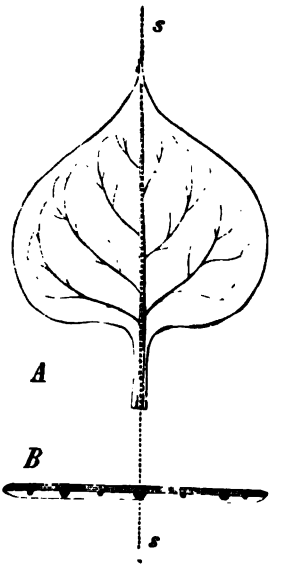


FIG. 127.—Diagram of a foliage leaf. *A*, Surface view. *B*, Transverse section; *s*, plane of symmetry. (After STRASBURGER.)

which is as a rule definitely dorsiventral and of a deeper green colour on the upper side, may be entire or divided (Fig. 122 *C*), or composed of a number of leaflets. Such compound leaves arise by a process of branching from the margins of the primordia (Fig. 122 *A*), or occasionally, as in the Palms, by splitting of the young lamina as it unfolds. The leaves of Monocotyledons are usually simple, while compound leaves are common among Dicotyledons.

A leaf-blade is termed PELTATE when the leaf-stalk appears to be inserted centrally (Fig. 242). The margin of simple leaves (Figs. 123 *lb*, 124 *sp*) may be ENTIRE or slightly divided, and in the latter case is described as SERRATE, DENTATE, etc. If more deeply divided the leaf is described as LOBED when the divisions do

not extend half-way to the middle of the leaf-blade, when they reach half-way as CLEFT (Fig. 135 *sb*), and when still deeper as PARTITE (Fig. 137 *l*). The lamina is PALMATE (Fig. 137) or PINNATE (Fig. 136, 1-5), according to whether the divisions are directed towards the base of the leaf-blade or towards the midrib. Only when the separate divisions are so independent that they appear as distinct leaflets borne on a common petiole or on the original midrib is the leaf spoken of as COMPOUND (Fig. 136, 1-5); in all other cases it is termed SIMPLE.

The leaflets of a compound leaf may be so segmented during their development as to resemble the main leaf, and in this way a leaf may be doubly or triply compound or more highly segmented. Simply pinnate or bi-pinnate leaves (Fig. 136) bearing leaflets on the two sides of the rachis of the first or second order are of frequent occurrence. The leaflets of a compound leaf may be entire or more or less deeply incised. They may be inserted directly on the rachis or be stalked, and in some cases, *e.g. Phaseolus* (Fig. 132 *fg*), *Robinia*, *Mimosa*, be provided with swollen pulvini at their bases.

In laminae, which become more or less branched during their development, the lateral divisions usually arise in basipetal order, *i.e.* proceeding from the tip towards the base, but the opposite (acropetal) succession or a combination of the two are also met with. The divisions of palmate and pinnate leaves of the Palms arise by a relatively late process of splitting within the originally entire, enlarging lamina. The direction of the dividing lines is determined by the folding of the young leaf-blade ([61]).

Sessile leaves usually clasp the stem by a broad base. Where, as in the case of the Poppy (*Papaver somniferum*), the leaf-base surrounds the stem, the leaves are described as AMPLEXICAUL; if, as in species of *Bupleurum*, it completely surrounds the stem, the term PERFOLIATE is used. If the bases of two opposite leaves are united, as in the Honeysuckle (*Lonicera caprifolium*), they are said to be CONNATE. Where the blade of the leaf continues downwards along the stem, as in the winged stems of the common Mullein (*Verbascum thapsiforme*), the leaves are distinguished as DECURRENT.

The leaf-blade is traversed by green nerves or veins which form a branched net-work. The thicker ribs project more or less from the surface on the lower side of the leaf, the upper surface often showing corresponding grooves. The finer veins become visible when the leaf-blade is viewed by transmitted light. Frequently the nerve in the middle line of the lamina is more strongly developed and is then termed the midrib; in other cases several equally developed main nerves are present (Fig. 122). Lateral nerves spring from the one or more main nerves (Fig. 126).

The course of the nerves determines what is known as the VENATION of the leaf. The leaves of most Coniferae are UNI-NERVED. In leaves with more numerous veins, the DICHOTOMOUS VENATION must be distinguished as a special type which is characteristic of many Ferns and is also found in *Ginkgo biloba*; there is no midrib present in this case. Most other leaves can be distinguished according to their venation as PARALLEL VEINED or NETTED VEINED. In parallel venation the veins or nerves run either approximately parallel with each other or in curves, converging at the base and apex of the leaf (Fig. 133 *s*); in netted veined leaves (Fig. 126) the veins branch off from one another, and gradually decrease in size until they form a fine anastomosing network. In leaves with

parallel venation the parallel main nerves are usually united by weaker cross veins. Netted or reticulately-veined leaves in which the side veins run from the median main nerve or MIDRIB are further distinguished as PINNATELY VEINED (Fig. 126), or as PALMATELY VEINED (Fig. 122, 135 *sb*), when several equally strong ribs separate at the base of the leaf-blade, and give rise in turn to a network of weaker veins. Parallel venation is characteristic, in general, of the Monocotyledons; reticulate venation, of Dicotyledons and of some Ferns.

Internal Structure.—In structure foliage leaves exhibit considerable variety but are usually markedly dorsiventral (bifacial), the tissues towards the upper side being different from those below (Figs. 127, 130).

Many leaves, however, are similarly constructed above and below (equifacial, centric, Figs. 187, 193). This is the case especially in forms which grow in relatively dry situations, exposed to strong sunlight, but also occurs in submerged aquatic plants.

(*a*) NERVES.—Within the nerves or veins one or more vascular bundles run. The abundant branching of these bundles to form a fine network is very characteristic of the leaf-blade and is shown clearly in leaf skeletons obtained by macerating leaves.

The structure of the vascular bundles in the lamina corresponds on the whole to that seen in the stem. In Phanerogams the bundles are usually collateral, and since they are continuations of the leaf-trace bundles from the stem the xylem is directed towards the upper, and the phloem towards the lower surface of the leaf.

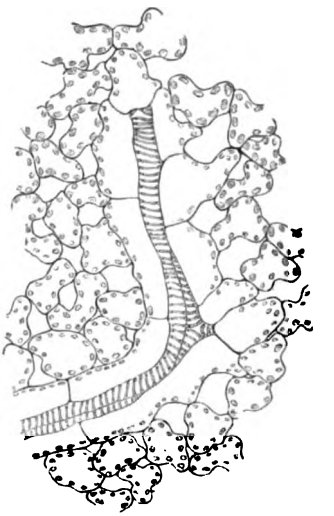


FIG. 128. — Termination of a vascular bundle in a leaf of *Impatiens parviflora*. (× 240. After SCHENCK.)

The xylem parenchyma of the bundles in the leaf usually forms flat plates, which in cross-section appear as radial rows of cells in the vascular tissues.

As the bundles continue to ramify in the leaf-blade they become smaller and simpler in structure. The vessels first disappear, and only spirally and reticulately thickened tracheides remain to provide for the water conduction. The phloem elements undergo a similar reduction. In Angiosperms, in which the sieve-tubes are accompanied by companion cells, the sieve-tubes become narrower, whilst the companion cells retain their original dimensions. Finally, in the cells forming the continuation of the sieve-tubes, the longitudinal division into sieve-tubes and companion cells does not take place, and TRANSITION CELLS are formed. With these the phloem terminates, although the vascular portion of the bundles still continues to be represented by short spiral tracheides. The ultimate branches of the bundles terminate blindly (Fig. 128).

The bundles are surrounded by parenchymatous sheaths, which are composed of a number of layers of cells in the thicker nerves but of a single layer only in the finer branches. The cells of these sheaths are as a rule elongated and have no intercellular spaces. Strands of sclerenchymatous fibres are frequently present on one or both faces of the bundle (Fig. 129, 1), especially on the phloem side. Here, in the case of the larger bundles, the strand of sclerenchyma is curved; in cross-section it occupies the projection of the rib to the under side, and serves to give rigidity against bending to the lamina. In some leaves strands of sclerenchyma also occur between the bundles (Fig 129, 1) and also at the leaf-margin. Such sclerenchymatous or collenchymatous strengthenings of the margin are protective against shearing forces that would tend to tear the lamina (Fig. 129, 2). Large leaf-blades

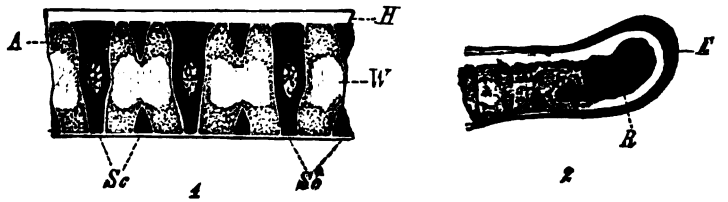


FIG. 129.—Leaf of *Phormium tenax*. 1. Transverse section; *Sc*, plates and strands of sclerenchyma; *A*, green assimilatory parenchyma; *H*, hypoderma serving for water-storage; *W*, colourless mesophyll (internal water-storage tissue). 2. Edge of the same leaf; *E*, thick brown epidermis; *R*, marginal strand of sclerenchyma fibres. (After NOLL.)

which lack such marginal protection are torn by the wind (*e.g.* the Banana).

(*b*) EPIDERMIS AND MESOPHYLL.—The foliage leaf is bounded on all sides by a typical epidermis. In this, especially on the under side, there are numerous stomata, while on the upper side they are often absent (*e.g.* in almost all deciduous trees).

On the under side there are on the average 100-300 stomata to the square millimetre, but in some cases more than 700 may occur. Isolateral leaves as a rule have stomata on both sides and floating leaves only on the upper surface.

The tissue of the leaf-blade between the upper and lower epidermis in the intervals between the ribs consists mainly of parenchyma and goes by the name of MESOPHYLL. The finer veins are embedded in it. Beneath the upper epidermis (Fig. 130 *ep*) come, as a rule, one to three layers of cylindrical parenchymatous cells elongated at right angles to the surface. These are called PALISADE CELLS (Fig. 130 *pl*), contain abundant chlorophyll, and have intercellular spaces between them. They constitute an assimilatory parenchyma. The cells often converge below in groups (Fig. 130) towards enlarged collecting cells (*s*).

In the leaves of many trees, *e.g.* the Copper Beech, differences in the thickness of the palisade layer are met with, its depth being much less in the "shade-leaves"

than in the "sun-leaves." According to NORDHAUSEN's investigations (62), however, no direct influence of the illumination exists. There are also plants (*e.g. Lactuca scariola*) which only form palisade cells in strongly illuminated leaves.

In some plants layers of cells placed parallel to the surface instead of at right angles to it are found in the usual situation of the palisade tissue. In the leaves of the Pine and some other plants the same position is occupied by large, more or less isodiametric cells the internal surface of which is considerably increased by foldings of the cell walls.

Below the palisade parenchyma comes what is known as the SPONGY PARENCHYMA (*sp*), which extends to the lower epidermis (*ep''*). The spongy parenchyma consists of irregularly-shaped cells with wide intercellular spaces and less chlorophyll than in the palisade

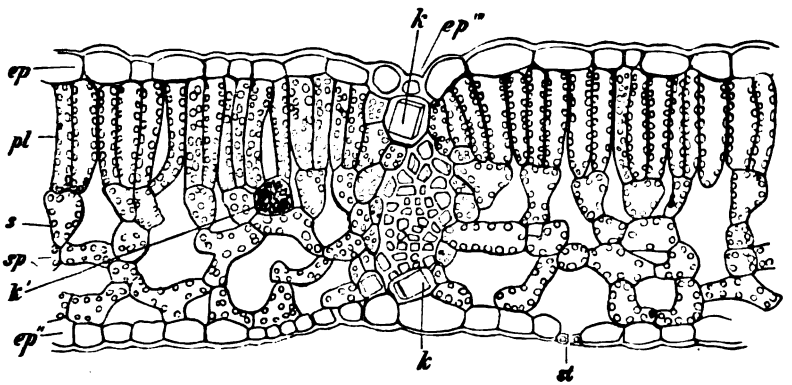


FIG. 130.—Transverse section of a leaf of *Fagus sylvatica*. *ep*, Epidermis of upper surface; *ep''*, epidermis of under surface; *ep'''*, elongated epidermal cell above a vascular bundle; *pl*, palisade parenchyma; *s*, collecting cells; *sp*, spongy parenchyma; *k*, idioblasts with crystals, in *k'* with crystal aggregate; *st*, stoma. (× 360. After STRASBURGER.)

tissue. The wide intercellular spaces stand in immediate relation to the stomata of the lower epidermis and serve for the transport of gases to the palisade cells.

HABERLANDT has estimated the number of chloroplasts per square millimetre of a leaf of *Ricinus* to be 403,200 in the palisade parenchyma and 92,000 in the spongy parenchyma. Thus in this case 82 per cent of the chloroplasts would belong to the upper and only 18 per cent to the lower side.

Colourless WATER-STORAGE TISSUE is frequently present in the mesophyll (Fig. 129 *W*). It may be surrounded by the assimilatory tissue or be situated externally to this below the epidermis. In the latter case the water-storage tissue usually consists of the more internal cells of a many-layered epidermis.

EPITHEMA and WATER-STOMATA (63).—The mesophyll of the leaf-blade in certain families of Monocotyledons and Dicotyledons forms peculiar structures between the swollen ends of vascular bundles and the epidermis. They are composed of small living cells with colourless cell sap, the intercellular spaces being filled with water. These masses of tissue go by the name of EPITHEMA and bring about the excretion of drops of liquid water. In this process their function is

mainly passive, since they represent places where the resistance to filtration is least. The tracheides terminate in this epithema, and in the overlying epidermis there is a peculiarly-constructed stomatal apparatus in the form of WATER-PORES (Fig. 131), which are of larger size than ordinary stomata. The guard cells usually lose their living contents and the pore then remains permanently and widely open. The thickened ridges so characteristic of the guard cells of ordinary stomata are usually lacking. The excreted liquid frequently contains calcium carbonate, which may remain as a white incrustation over the water-pores, as, for example, on the leaf margin in many species of *Saxifraga*.

At the tip of young leaves and of their marginal teeth such water-pores and epithemata frequently occur, but are dried up on the mature leaf. Water-pores also are found at the leaf-tips of submerged plants from which ordinary stomata are absent. They tend to perish early, breaking down with the adjoining tissue to leave open pits by which water and dissolved substances may be expressed.

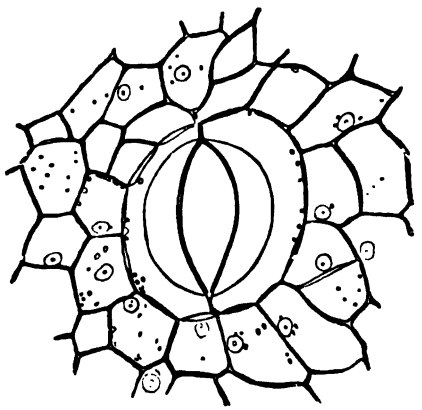


FIG. 131.—Water-pore from the margin of a leaf of *Tropaeolum majus*, with surrounding epidermal cells. (× 240. After STRASBURGER.)

Functions of the Leaf-blade.—The leaf-blades, as already mentioned, are the most important organs of nutrition, *i.e.* assimilation, and also of transpiration in cormophytes. Their form and structure, their arrangement, and the position they assume with regard to the direction of the light, correspond to this. Since the decomposition of carbon dioxide is dependent both on light and on the presence of chlorophyll, the green colour of the lamina, the large surface exposed by it, its relative thinness and dorsiventral construction are readily understood. The large surface enables a greater number of cells containing chlorophyll to be exposed to the light without shading one another; it also enables the carbon dioxide to be obtained from the small proportion in the atmosphere, and at the same time facilitates the loss of water vapour in transpiration. Since the passage of light through a few layers of cells filled with chlorophyll renders it ineffective for decomposing carbon dioxide in the deeper layers, the assimilatory tissue is placed towards the upper surface of the leaf-blade. The carbon dioxide is mainly taken into the leaf through the stomata of the lower surface. It can thus diffuse rapidly through the wide intercellular spaces of the spongy parenchyma, which is essentially a ventilating tissue, to the active assimilatory tissue of the upper side. This will take place more rapidly the thinner the leaf is.

The extensively-branched network of vascular bundles ensures the

rapid passage of the products of assimilation from the assimilatory cells of every part of the leaf to the stem. At the same time it facilitates the most direct supply of water to all parts of the transpiring leaf-blade; the leaf-blade serves for giving off water, while the stem serves for conduction of water. Lastly, the venation increases the rigidity of the lamina.

It has been seen that the leaves are so arranged on the stem that the leaf-blades, which on erect shoots have a more or less horizontal position, are exposed to the light with the least shading by one another. Many leaves can place their blades at right angles to the incident light by their power of movement. In the case especially of dorsiventral, plagiotropous branches the leaf-blades seen from above are found to fit together more or less closely in a LEAF MOSAIC, the upper surfaces of all being exposed to the light.

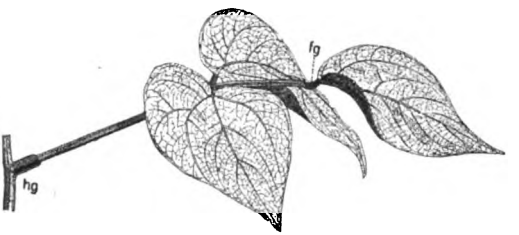


FIG. 132.—Imparipinnate leaf of *Phaseolus* with pulvini. *hg*, Main pulvinus at base of petiole; *fg*, pulvinus of one of the pinnae. (½ nat. size.)

(b) The Leaf-stalk usually resembles a stem, and in its internal construction agrees with the midrib of the leaf-blade or sometimes with the stem. Typical assimilatory tissue is wanting, and the vascular bundles in the case of Angiosperms are usually arranged in an arc open above. The leaf-stalk serves to carry the leaf-blade away from the stem and to place it suitably with respect to the light.

These movements of adjustment of the leaf to the light are sometimes carried out by special localised swellings at the base or the summit of the leaf-stalk, or in both situations. These LEAF-CUSHIONS or PULVINI work like hinges and occur in many Leguminosae (Fig. 132).

Stalked leaves, which are more frequent among Dicotyledons than in Monocotyledons, either have the lamina sharply marked off from the petiole or the one passes gradually into the other, the petiole appearing more or less winged. When leaves are arranged in a rosette the stalks of the lower leaves are often so long that the laminae borne on them are not shaded by the upper leaves. This is shown very beautifully in the floating rosettes of the Water Nut (*Trapa natans*).

(c) The Leaf-base (64).—When the leaf-base of a foliage leaf is specially formed, it usually serves to protect the bud and the younger leaves, enclosing the bud after the leaf-blade has unfolded.

Stipules are frequently developed from the leaf-base; they stand one on either side of the leaf to which they belong, forming a pair. They may be inconspicuous (Fig. 124 *nb*) or larger, and yellow or green in colour. When they serve only to protect the bud they are

usually yellowish or brown, more simple in their structure than the leaf-blade, and are soon shed.

The two stipules in such cases are frequently more or less completely united to form a single structure standing in the axil of the leaf. They may also surround the stem and form a closed tube which encloses the younger leaves of the bud. This is the case in the India Rubber plant (*Ficus elastica*) which is frequently grown in dwelling-houses; in this the sheaths are broken off at their bases and carried up on the next younger leaf as it unfolds. In the Polygonaceae they are broken through and remain as dry sheaths (ochrea, Fig. 617) surrounding the stem.

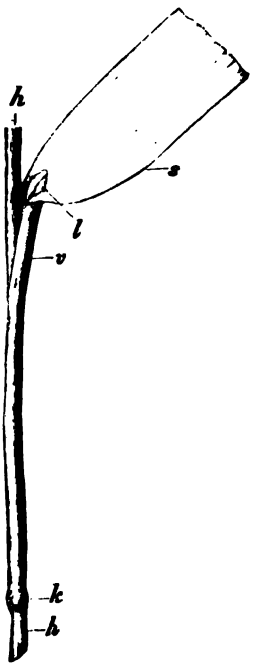


FIG. 133.—Part of stem and leaf of a grass. *h*, Haulm; *v*, leaf-sheath; *k*, swelling of the leaf-sheath above the node; *s*, part of leaf-blade; *l*, ligule. (Nat. size. After SCHENCK.)

When the stipules take part in the assimilation of carbon dioxide they are green and resemble the leaf-blade in structure (Fig. 209).

In some species of *Galium* in which the stipules completely resemble the leaf-blades, there is an appearance of whorls of four, six, or eight leaves; in reality the arrangement of the two leaves is decussate, each leaf having one or more pairs of stipules according to the species. Only the two leaves have buds in their axils.

The leaf-base may form a sheath; this is more commonly the case in Monocotyledons than in Dicotyledons. In the Grasses (Fig. 133 *v*) the sheath is split along one side, but in the Cyperaceae it is closed. The sheath of the grass leaf, which encloses and supports the lower delicate portion of the still growing internode, continues at the base of the sessile lamina into a membranous outgrowth called the ligula (*l*); at its base immediately above the node the sheath is swollen (Fig. 133 *k*).

Anisophylly and Heterophylly.—Some plants bear diversely-formed foliage leaves either in different zones of the stem (HETEROPHYLLY, Fig. 135) or in the same zone, but on the two sides of the shoot which thus becomes dorsiventral (ANISOPHYLLY, Fig. 134). Asymmetry of the leaves is often associated with anisophylly. Many water-plants exhibit heterophylly, having ribbon-shaped or highly-divided submerged water-leaves adapted to life in water and less divided stalked aerial leaves (Fig. 135). The leaves which the Ivy

forms on the flowering shoots are essentially different in form from those which the plant has previously borne. This difference is even more marked in *Eucalyptus globulus*, which first bears oval sessile leaves and then sickle-shaped leaves. Not uncommonly the lowest leaves of the seedling (juvenile or primary leaves) are more simply formed than the later leaves. The opposite case is illustrated by *Acacia* (Fig. 136).

B. The Seed-leaves or Cotyledons may be stalked or sessile, and are always more simple in form than the foliage leaves. They often, however, exhibit the same plan of segmentation.

FIG. 134.—*Selaginella Martensii*, Anisophylly of the dorsiventral shoot. On the upper side of the stem are two rows of smaller asymmetrical green leaves and on either flank a row of larger asymmetrical leaves (slightly magnified).

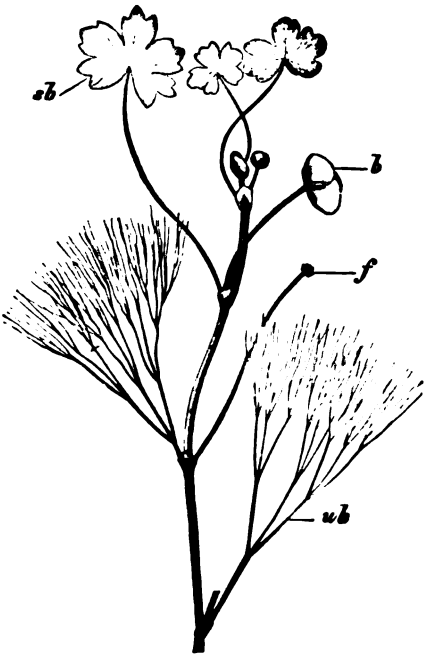


FIG. 135.—*Ranunculus aquatilis*. *ub*, Submerged leaves; *sb*, floating leaves; *b*, flower; *f*, fruit. (Reduced. After SCHENCK.)

The cotyledons may remain below the soil enclosed in the seed-coat (HYPOGEAL). In this case they are usually fleshy structures serving to store reserve food material and are composed largely of storage parenchyma. EPIGEAL cotyledons, which burst the seed-coat and appear above ground, tend to become green and then for a period assimilate carbon dioxide like the foliage leaves. In Monocotyledons, which have a single cotyledon, only the sheath of this as a rule emerges from the seed. It may remain below ground and colourless, or grow up and turn green.

C. The Scale Leaves and Bracteal Leaves, while indistinguishable from the foliage leaves in the early stages of development, are less

differentiated than these when mature, being usually scale-like and sessile. They are developed by enlargement of the primordia, mainly from the leaf-base, while the lamina remains more or less undeveloped (Fig. 124 *1-6*, Fig. 137). Scale leaves, either colourless or green, often occur on the aerial shoots before the foliage leaves (Fig. 123 *nd*). They are also the only foliar organs on rhizomes, appearing as hardly visible and usually short-lived scales, while in accordance with the development in darkness foliage leaves are wanting (Fig. 123 *ws*, Fig. 138). The bracteal leaves, on the other hand, resemble in construction the scale leaves on aerial shoots, but are often variously coloured and tend to succeed the foliage leaves as the subtending leaves and bracts of the flowers or inflorescences. The internal structure of both scale leaves and bracts is simpler than that of the foliage leaves. They hardly take part in the nutritive processes, but are usually protective structures for the young leaves or the buds. They are, however, connected with the foliage leaves by intermediate forms (Figs. 124, 137).

FIG. 136.—Seedling of *Acacia pycnantha*. The cotyledons have been thrown off. The foliage leaves *1-4* are pinnate, the following leaves bipinnate. The petioles of leaves *5* and *6* are vertically expanded; and in the following leaves, *7*, *8*, *9*, modified as phyllodes, bearing nectaries, *n*. (About ½ nat. size. After SCHENCK.)

That scale leaves and bracts are to be regarded as arrested forms of foliage leaves is shown not only by the developmental history but by the possibility of deriving foliage leaves from their rudiments or primordia. Thus GOEBEL succeeded in causing leaf primordia that would have formed scale leaves to become foliage leaves by removing the apex and stripping the leaves from the shoots. Subterranean stems, when forced to develop in the light, form foliage leaves from the primordia which in the earth would have become scale leaves. In their internal structure, however, the scale leaves and bracts are not merely arrested foliage leaves but frequently exhibit special differentiations connected with their particular functions ([65]).

8. Duration of Life of Leaves.—In many plants the leaves have a shorter life than the stems on which they are borne. The leaves in such plants are shed from the stems (LEAF-FALL) or, in the case of

subterranean shoots, decay while still attached. The leaves and stems of the aerial shoots of herbs die off together. LEAF-SCARS mark the places where the fallen leaves were attached to the stem. Plants in which the foliage leaves remain active for several seasons are called EVERGREEN in contrast to DECIDUOUS forms.

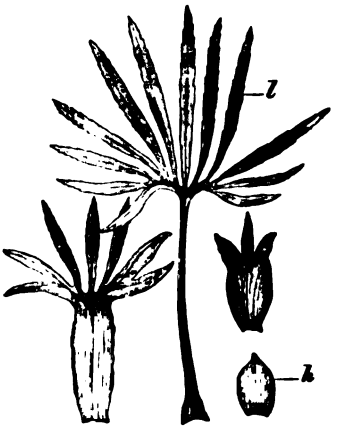


FIG. 137.—*Helleborus foetidus*. Foliage leaf (*l*) and intermediate forms between this and the bract (*h*). (Reduced. After SCHENCK.)

The fall of the leaves in phanerogamic woody plants is effected by means of a parenchymatous ABSCISS LAYER which is formed at the base of the leaf-stalk shortly before the leaf is shed. In this region all the mechanical tissues of the petiole are greatly reduced, only the vessels being lignified. The separation of the leaf results from the rounding off of the cells of the absciss layer, the middle lamellae becoming mucilaginous, while the vessels and sieve-tubes are broken through. The protection of the leaf-scar is effected by the cells exposed by the wound becoming transformed into a lignified cutis tissue and, later, by the formation of a layer of cork produced from a cork cambium and continuous with that covering the stem.

D. The Branching of the Shoot ([56, 66]). — The more foliage leaves that can be exposed to the sunlight on a shoot the greater will be the amount of organic substance formed by assimilation. In this respect, as will be evident, a branched system of shoots is greatly superior to a single erect shoot. The former can expose leaf-surfaces to the full sunlight over a much greater area.

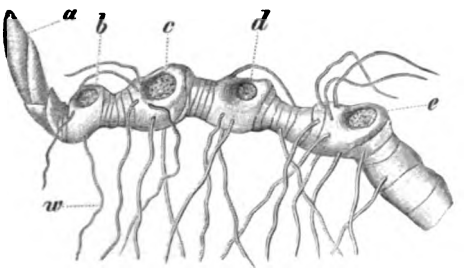


FIG. 138.—Rhizome of *Polygonatum multiflorum*. *a*, Bud of next year's aerial shoot; *b*, scar of this year's, and *c*, *d*, *e*, scars of three preceding years' aerial shoots; *w*, roots. (½ nat. size. After SCHENCK.)

As in thalloid plants the branching of the shoot can happen in two ways. Rarely the shoot forks, dividing into two daughter axes (DICHOTOMY). Usually the branching is LATERAL, the daughter axes being thus formed on the main axis which continues its growth.

A. Dichotomous Branching. — This is confined to the shoots of some Lycopodiaceae.

In such Club-Mosses, when a shoot is about to divide into two equal branches,

the circular outline of the growing point, in which no apical cell is recognisable, becomes elliptical. In the position of the foci of this ellipse the two new growing points project (Fig. 139). The successive dichotomies may take place in planes at right angles to one another, in which case the branch-system does not lie in one plane as in the diagram in Fig. 82 *a*.

Not uncommonly in plants of this kind

FIG. 139.—Longitudinal section of a bifurcating shoot (*p*) of *Lycopodium alpinum*, showing equal development of the rudimentary shoots, *p'*, *p''*; *b*, leaf-rudiments; *c*, cortex; *f*, vascular strands. (× 60. After HEGELMAIER.)

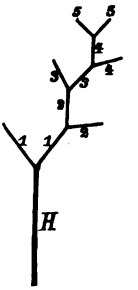


FIG. 140.—Sympodium arising from successive dichotomies.

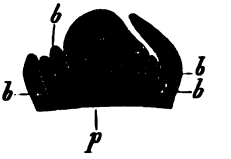


FIG. 141.—Bifurcating shoot (*p*) of *Lycopodium inundatum*, showing unequal development of the rudimentary shoots, *p'*, *p''*; *b*, leaf-rudiments. (× 40. After HEGELMAIER.)

(*e.g.* in *Selaginella*) the branch-system deviates from the type described in that only one of the branches of each fork grows on further and again dichotomises (Fig. 140). If all the branches that in this way continue the branching are placed nearly in the same direction to which the other branches stand obliquely, the branch-system which results may readily be confused with racemose branching (Fig. 82 *b*). The main axis is, however, only apparently single, each portion being a daughter axis of the portion that precedes it. Such an apparent axis is distinguished as a sympodium from a true main axis (monopodium), and the branching is sympodial and based on dichotomy.

All transitions from dichotomous to lateral branching are seen in the Lycopodiaceae. Some species form from the outset two growing points of unequal size, the smaller being soon displaced laterally in respect to the larger one (Fig. 141).

B. Lateral Branching. (a) Place of Origin of the Lateral Buds.—On shoots composed of axis and leaves the lateral branches as a rule occur on the axis or at the extreme base of the leaf. They are usually developed at the growing point of the parent shoot in acropetal succession as exogenous outgrowths of the surface in the same way as the leaf primordia arise (Fig. 98 *g*). The positions in which the lateral shoots are developed are usually strictly determined. In Pteridophyta they frequently arise beside the leaf primordia, but in Phanerogams, as a rule, where the upper side of the papilla forming the young leaf passes into the tissue of the growing point, *i.e.* in the LEAF AXIL. In some cases the branch is more on the leaf-base, in others it is distinctly on the main stem.

The primordium of a lateral branch may arise from the tissue of the axis close above the leaf primordium and either after the origin of the latter (Fig. 142 *I*)

or before the leaf has developed. In the latter case the leaf-rudiment arises from the tissue to the lower side of the branch primordium (Fig. 142 *III*). On the

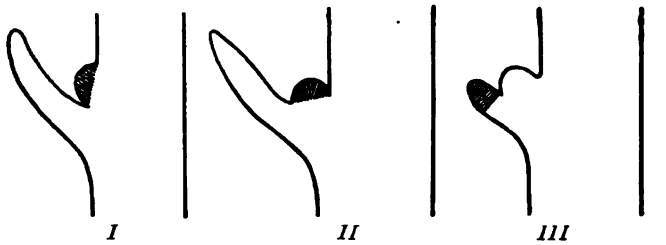


FIG. 142.—Diagrams of the developmental relations between the leaf primordium and the axillary shoot. (After GOEBEL.)

other hand, the branch may be formed from the young leaf primordium (Fig. 142 *II*). Lastly, in dorsiventral shoots extra-axillary shoots may arise laterally from the leaf primordia.

In the longitudinal section of a growing point in Fig. 98 the youngest rudiment of a lateral shoot (*g*) is already visible, projecting in the axil of the uppermost leaf. In the axils of the following leaves the branch primordia, since they arose in acropetal succession, are larger and have begun to form their leaves. The shoots developed from such AXILLARY BUDS are termed AXILLARY SHOOTS; the bud which terminates the growing end of the main shoot is termed, in contrast to the axillary buds, a TERMINAL BUD. The leaf, in the axil of which a bud stands, is its SUBTENDING LEAF (Fig. 144 *db*). The plane passing through the midrib of this leaf and the parent axis is the MEDIAN PLANE of the leaf. Usually the axillary bud is situated in the median plane of its subtending leaf, but it may be displaced laterally. It is the rule in Angiosperms that each foliage leaf has a single axillary bud; in some Gymnosperms, on the other hand, there is not an axillary bud to every leaf.

FIG. 143.—*Samolus valerandi*, each axillary shoot (*a*) bearing its subtending leaf (*t*), and terminating in a fruit. (Nat. size. After SCHENCK.)

As a rule, only one shoot develops in the axil of a leaf, yet there are instances where it is followed by additional or ACCESSORY SHOOTS, which either stand over one another (serial buds), as in *Lonicera*, *Gleditschia*, *Gymnocladus*, or side by side (collateral buds), as in many Liliaceae, *e.g.* species of *Allium* and *Muscari*. A displacement from the position originally occupied by the members of a shoot frequently results from intercalary growth. A bud may thus, for example, become pushed out of the axil of its subtending leaf, and thus apparently have its origin higher on the stem; or a subtending leaf in the course of its growth may carry its axillary bud along with it, so that the shoot which afterwards develops

seems to spring directly from its subtending leaf; or, finally, the subtending leaf may become attached to its axillary shoot, and, growing out with it, may thus appear to spring from it (Fig. 143).

It is the rule in Phanerogams that normal shoots arise from the embryonic tissue of the growing point of the parent shoot. When they are apparent at a greater distance from the apex it can usually be shown that embryonic substance has been reserved at the proper points for their formation.

Shoots developing in predetermined positions on young parts of the plant are designated NORMAL, in contrast to ADVENTITIOUS SHOOTS, which are produced irregularly from the old or young portions of a plant, such as stems, roots, or leaves, and usually arise from permanent tissue which returns to the meristematic condition. Adventitious shoots, which arise from the older parts of stems or roots, are almost always ENDOGENOUS. They must penetrate the

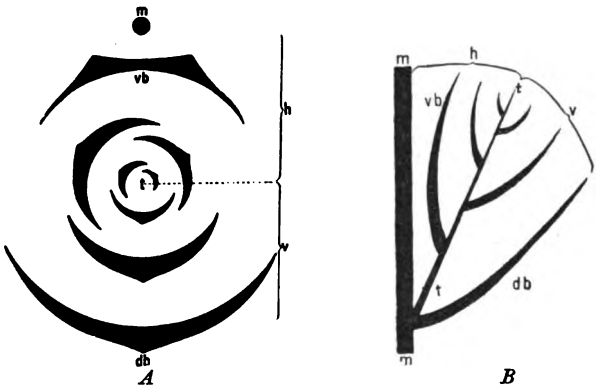


FIG. 144.—*A*, ground plan or diagram, and *B*, lateral view of a lateral bud of a Monocotyledon with a divergence of ½; *m*, parent axis; *db*, subtending leaf borne on this; *t*, the daughter axis; *vb*, bracteole on this; *h*, posterior, and *v*, anterior sides of the daughter shoot.

outer portions of their parent shoot before becoming visible. Adventitious shoots formed on leaves, however, arise, like normal shoots, exogenously.

Such adventitious shoots frequently spring from old stems, also from the roots of herbaceous plants (*Brassica oleracea*, *Anemone sylvestris*, *Convolvulus arvensis*, *Rumex Acetosella*), or of bushes (*Rubus*, *Rosa*, *Corylus*), or of trees (*Populus*, *Ulmus*, *Robinia*). They may even develop from leaves, as in *Cardamine pratensis*, *Nasturtium officinale*, and a number of Ferns. An injury to a plant will frequently induce the formation of adventitious shoots, and they frequently arise from the cut surface of stumps of trees. Gardeners often make use of pieces of stems, rhizomes, or even leaves as cuttings from which to produce new plants ([67]). When the buds in this case do not arise from existing growing points but are new-formed from permanent tissue, the process is spoken of as REGENERATION (cf. the section on Physiology).

(b) The Position of the Leaves of Lateral Buds.—When the relations of position in a lateral branch of any order are to be

examined the branch is placed with its subtending leaf towards the observer (ANTERIOR), and the parent axis POSTERIOR (Fig. 144 *A*), and so that the median plane of the subtending leaf coincides with that of the observer. Structures on the lateral branch, which are directed towards its subtending leaf, are termed anterior, those towards the parent shoot posterior, while right and left refer to structures lying to either side of the median plane of the subtending leaf in the TRANSVERSE PLANE.

Independently of the phyllotaxis, the lowest leaves of a lateral bud which come next above the subtending leaf tend to occupy a definite position in relation to the latter and to the parent axis. They connect the phyllotaxy of the lateral branch with that of the main shoot. In Monocotyledons there is one such BRACTEOLE (Fig. 144 *vb*), while in Dicotyledons there are two bracteoles; they are usually scale or bracteal leaves. The bracteole in Monocotyledons is median and stands on the posterior side of the branch towards the main axis. It frequently has two lateral veins appearing as keels, while a middle vein is wanting (Fig. 144 *A*); it may thus be regarded as arising from the union of two lateral bracteoles ([68]). In Dicotyledons the two bracteoles (α and β) stand as a rule right and left in the transverse plane, the later leaves following in a different arrangement.

Apart from this the lateral buds may show the same leaf arrangement as the parent axis or may differ from this.

When the phyllotaxy is spiral the genetic spiral of the branch may either run in the same direction as that of the main axis (homodromous) or in the opposite direction (antidromous).

(c) Construction of the Branch System.—The general aspect or habit of every shoot-system depends, in addition to the direction of growth of its main axis, on the following features: the number of orders of lateral axes that develop; the position on the main axis of the buds which grow out as lateral branches; the intensity of the growth and the orientation of the lateral axes of various orders in relation to one another and to the parent axis. The variety in the general habit of the shoot-systems frequently also stands in relation to the mode of life of the plants.

1. DIRECTION OF GROWTH OF THE MAIN AXIS OF THE SHOOT-SYSTEM.—This, in the first place, determines the general type of the shoot-system.

If the main axis stands at right angles to the soil, the shoot is termed ORTHOTROPOUS and the plant erect. In this case the more or less plagiotropous and dorsiventral lateral branches tend to be distributed radially when the plant is growing freely. If the main axis is growing obliquely or horizontally, and is thus PLAGIOTROPOUS, the arrangement of the branches is usually dorsiventral; when such a main axis with its lateral branches remains on the surface of the soil or grows horizontally beneath this, the plant is CREEPING. The lateral branches tend

to come from the flanks and the roots from the lower surface of the main stem. In such a plant, when lateral branches grow up at right angles to the soil, they behave as regards their further branching like erect plants.

2. THE ORDER OF SEQUENCE OF SHOOTS.—If the vegetative cone of the primary axis of a plant, after reaching maturity, is capable of reproduction, a plant with but one axis will result, and the plant is designated UNIAXIAL or HAPLOCAULESCENT. Usually, however, it is not until a plant has acquired axes of a second or third order, when it is said to be DIPLOCAULESCENT or TRIPLOCAULESCENT, or of the *n*th order, that the capacity for reproduction is attained. A good illustration of a plant with a single axis is afforded by the Poppy, in which the first shoot produced from the embryo terminates in a flower. As an example of a triplocaulescent plant may be cited the common Plantain (*Plantago major*), whose primary axis produces only foliage and scale leaves; while the secondary axes give rise solely to bracteal leaves, from the axils of which finally spring the axes of the third order, which terminate in the flowers. In the case of trees, only shoots of the *n*th order can produce flowers. Thus a division of labour commonly occurs in a branched plant, which finds its expression in differences of form between the successive shoots. These differ in appearance according to the special function performed by them, whether nutrition, storage, or reproduction. In addition to the essential members in the succession of shoots developed in a determined order, there are non-essential members which repeat forms of shoot already present. These may appear simultaneously with the essential shoots, and serve to increase the size of the plant, as in many annuals; in many perennial plants they arise as yearly innovations on the stock.

3. THE DISTRIBUTION OF UNFOLDING BUDS.—Only in relatively few cases, as, for example, in herbs, do all the lateral buds of a main axis proceed to grow on as shoots. As a rule many more lateral buds are formed than ever unfold. The remainder become DORMANT BUDS or perish. It would be a needless or even injurious expenditure of material on the part of the plant were all the buds to expand, since the branches would overshadow one another and some would perish.

Almost all trees possess, especially in the lower region of each annual growth, such dormant buds, which remain for a longer or shorter period capable of further development and can unfold under special conditions. The dormant buds of the Oak, Beech, etc., may be a hundred years old. The shoots that arise on old stems often come from these buds and are thus not adventitious.

The unfolding of lateral buds may proceed acropetally or basipetally, or exhibit no definite order. On highly-branched shoot-systems the more peripheral buds are favoured since they have the best opportunity of favourable exposure of the leaves to the light.

Nearly all our native trees form only resting buds through the summer while the main shoots are elongating. Later, usually at the commencement of a new period of growth, some of the uppermost buds formed in the preceding season grow into lateral branches. These branches may form a whorl or an apparent whorl (*Araucaria*, *Pinus*); more commonly the highest buds form long shoots while those below them become short shoots (Pear, Apple). In other shoots, especially those that grow erect, every second, third, or fourth, etc., bud unfolds

so that the resulting shoots are regularly arranged at similar distances from one another both longitudinally and laterally.

The habit of the branch-system depends on the distribution of the expanding buds, whether this is alternate or in whorls. When the buds are opposite a kind of dichotomous branching results as in the Horse Chestnut or the Elder.

4. DIRECTION AND INTENSITY OF GROWTH OF THE LATERAL BRANCHES in relation to one another. The lateral angle between adjacent lateral branches on an orthotropous branch may be very constant in any kind of plant (*e.g.* in *Araucaria* or *Pinus*). On the other hand, the intensity of growth of the lateral axes on the same main axis may show much variety. Frequently, with the appearance of a division of labour, only some of the branches are of unlimited growth, the others forming short shoots. The latter have usually a shorter life, tend not to branch, and do not take part in the persistent branch-system of the tree. In the Larch, for example, the short shoots form short rosettes of needles on the older shoots of unlimited growth.

5. DIRECTION AND INTENSITY OF GROWTH OF THE LATERAL BRANCHES IN RELATION TO THE MAIN AXIS. DIFFERENT TYPES OF LATERAL BRANCHING. — The angle at which the lateral branch is inclined to its main axis also tends to be very constant in any species (*e.g.* Pine).

The lateral branches may grow at the same rate as the parent axis, or less rapidly, or much more rapidly. In the last case they take precedence of the main axis, the growth of which may cease entirely, while one or more lateral branches take over the continuance of the branching. Diversity in the resulting branch-systems must evidently result from such differences in the growth of the daughter and parent axes. This has led to the distinction of various types of lateral branching, a knowledge of which is indispensable to the understanding of the morphological construction of the higher plants. The differences are especially well seen when the branches are close, as in the region where the reproductive organs or flowers are borne as lateral branches. The INFLORESCENCES may therefore serve as favourable examples of the different types of branching.

The bracts and bracteoles in the inflorescence are usually developed as scale leaves and do not resemble the foliage leaves. They do not serve for assimilation but only for the protection of the young lateral branches in their axils. If the branching of a lateral branch is continued, this proceeds as a rule from the axils of the bracteoles. It is further characteristic of many inflorescences that the axillary buds of all the bracts are developed further. Owing to this the inflorescences, in contrast to the vegetative shoot-systems, form crowded branch-systems, very numerous flowers being formed in a small space.

(*a*) The term **racemose branching** is applied when the main axis grows MORE ACTIVELY than the lateral axes of the first order, and these in turn more actively than the branches of the second order arising on them; also when the main axis grows as actively as its

daughter axes. In the former case a true main axis or MONOPODIUM can be followed throughout the entire branch-system (cf. Fig. 82 *b*). Such typical MONOPODIAL BRANCHING is exhibited, for example, by the Pine and other Conifers with a pyramidal outline; the radial orthotropous main shoot grows vertically upwards under the influence of gravity (cf. p. 339), while the dorsiventral lateral branches of the first order diverge on all sides horizontally from the main axis. If the lateral branches

FIG. 145.—Spike of *Plantago lanceolata*. (After DUCHARTRE.)

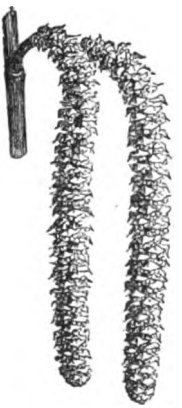


FIG. 146.—Catkin of *Corylus americana*. (After DUCHARTRE.)

FIG. 147.—Raceme of *Linaria striata*. *d*, Bracts. (After A. F. W. SCHIMPER.)

of the first order grow erect, as in the Cypress and in many shrubs, there may be no difference in length between them and the main axis; the branch-system has in such cases an oval or spherical form.

The **racemose inflorescences** may be divided in the following way:

I. **The main axis grows more strongly than the lateral axes.**

(*a*) **Lateral axes unbranched.**

1. RACEME: stalked flowers borne on an elongated main axis (Fig. 147, Fig. 150 *A*).
2. SPIKE: flowers sessile on an elongated main axis (Fig. 145, Fig. 150 *B*). A spike in which the axis is thickened and succulent is termed a SPADIX; a spike which, after flowering or after the fruits have ripened, falls off as a whole is a CATKIN (Fig. 146).

(*b*) **Lateral axes branched.**

3. PANICLE: a main axis bearing racemes laterally (Fig. 150 *E*, Fig. 149).

II. The main axis grows as strongly as the lateral axes.

4. UMBEL: a whorl of lateral axes bearing flowers on a main axis which grows to the same length and ends in a flower (Fig. 150 *C*, Fig. 148).
5. COMPOUND UMBEL: an umbel which has small umbels in place of the single flowers (Fig. 150 *F*).
6. CAPITULUM or HEAD: flowers sessile on a shortened main axis (Fig. 150 *D*).

(*b*) The term **cymose branching** is applied when the main axis grows LESS STRONGLY than the lateral axes, which continue the branching and in their turn are overtopped by the branches they bear. The resulting appearance differs according to whether several, equally strong, lateral axes of the same order, or only one lateral axis, continue the branch-system. In the latter case an apparent main axis or SYMPODIUM is formed.

In many cases of cymose branching the parent axis not merely grows more slowly than the daughter axes but its tip dies or is cast off. This happens in many of our trees such as the Willow or the Lime.

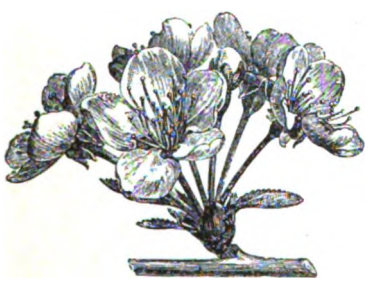


FIG. 148.—Umbel of the Cherry. (After DUCHARTRE.)

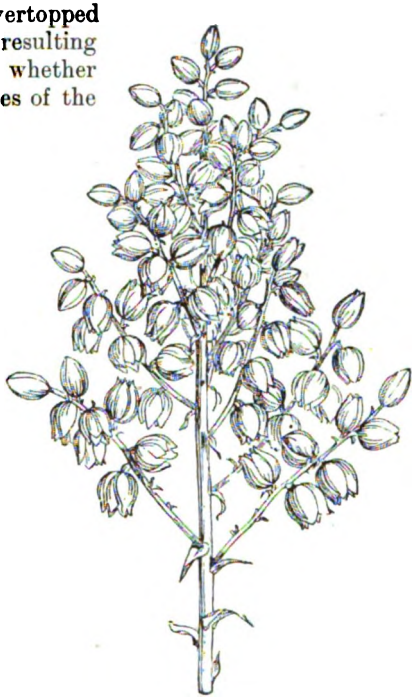


FIG. 149.—Panicle of *Yucca filamentosa*. (After A. F. W. SCHIMPER. Reduced.)

I. If more than two lateral branches of the same order continue the branching the term PLEIOCHASIUM is used. Such lateral branches are usually approximated to the upper end of the parent axis and radiate on all sides obliquely upwards, in some cases being arranged in a whorl. The inflorescence of *Euphorbia* affords an example.

II. If two lateral branches of the same order continue the branching and stand opposite to one another, forming an acute or right angle, the term DICHASIUM is used. This is shown diagrammatically in Fig. 151, with which the dichasial inflorescence in Fig. 153 may be compared. A branch system of this kind, another example of which is afforded by the Mistletoe, which grows parasitically on trees, simulates a dichotomy. The successive pairs of lateral branches do not lie in one

plane as in the diagram but stand at right angles to one another so that they diverge on all sides. Only a ground plan (Fig. 155 *E*) can therefore represent the true arrangement of the members of the branch-system.

III. When the branching is continued by a single lateral branch the term

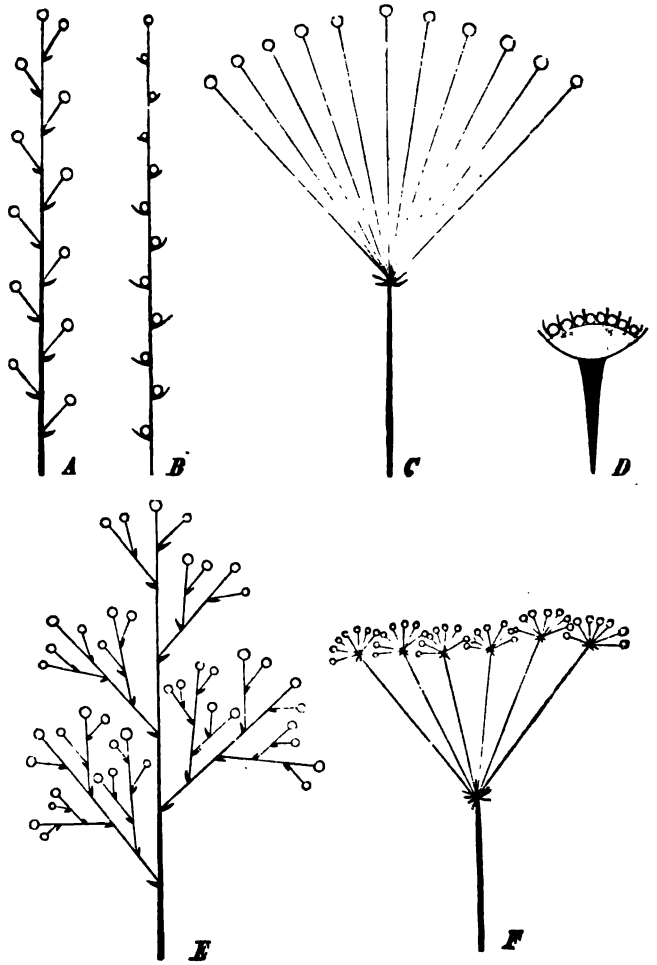


FIG. 150.—Diagrams of racemose inflorescences. *A*, Raceme. *B*, Spike. *C*, Umbel. *D*, Capitulum. *E*, Panicle. *F*, Compound umbel. (After KARSTEN.)

MONOCHASIUM is used. Frequently this branch continues the direction of the parent shoot, the tip of which is displaced to one side (Fig. 152). In this way a branch-system with a sympodial axis composed of lateral members of successive orders is formed, as was seen to be the case sometimes in dichotomous branching (p. 119 ff.). Such a branch-system may closely resemble monopodial branching,

especially when, as is frequently the case, the sympodium stands vertically and the arrested ends of the branches appear as if borne laterally upon it. They are distinguishable from truly lateral branches, however, by the regular absence of a subtending leaf, while a leaf which stands opposite to each apparent branch is really the subtending leaf of the daughter shoot that continued the sympodium (cf. Fig. 152). The further branching may also be sympodial. The branching of many trees, such as the Lime and Beech, is of this nature, but the sympodial construction is not recognisable in the stems and branches. It remains evident, however, in many subterranean shoots such as the rhizome of *Polygonatum multiflorum* (Fig. 138). The terminal bud of each year's growth becomes the aerial shoot, while an axillary bud continues the growth of the rhizome in the soil.

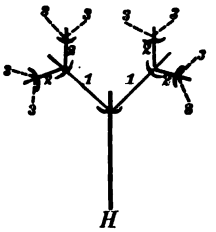


FIG. 151.—Diagram of the Dichasium. *H*, Axis of the seedling; *1*, *2*, *3*, daughter axes of the corresponding first, second, and third orders.

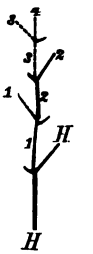


FIG. 152.—Diagram of the Monochasium. Cf. Fig. 151.

According to the relation of the lateral shoots of different orders to each other

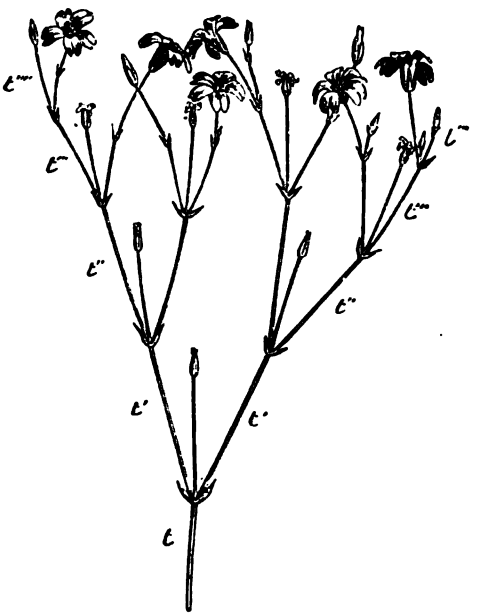


FIG 153.—Cymose inflorescence (dichasium) of *Cerastium collinum*. *t*-*t''''*, Successive axes. (After DUCHARTRE.)

FIG. 154.—*Heliotropium Curassavicum*, Cincinnus. (After ENGLER-PRANTL.)

there arise monochasial branch-systems of diverse and very characteristic construction. The branching frequently proceeds from the axil of a bracteole.

A. The median plane of all the lateral shoots may coincide with the median plane of the lateral shoot of the first order.

(α) The successive lateral branches are on the anterior side of the parent axis, *i.e.* between the latter and the subtending leaf (cf. p. 121). In lateral view they thus fall on the same side, DREPANIUM (Fig. 155 *C*, *D*).

(β) The successive axes stand on the posterior side of the parent axis (cf. p. 123) and in lateral view appear alternately right and left, RHIPIDIUM (Fig. 155 *A*, *B*).

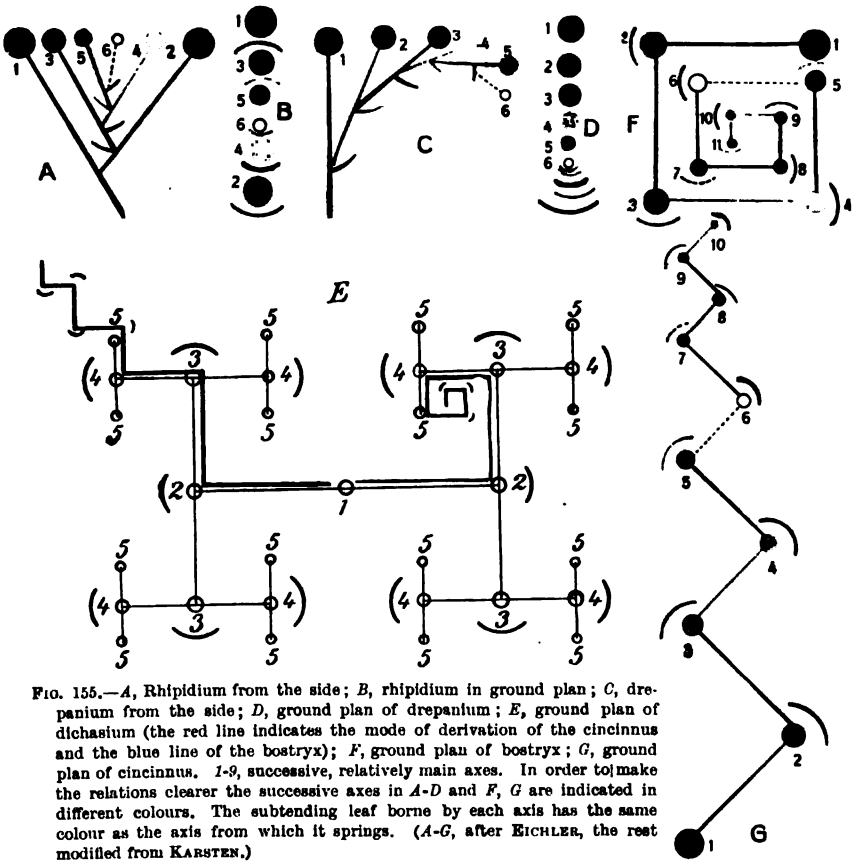


FIG. 155.—*A*, Rhipidium from the side; *B*, rhipidium in ground plan; *C*, drepanium from the side; *D*, ground plan of drepanium; *E*, ground plan of dichasium (the red line indicates the mode of derivation of the cincinnus and the blue line of the bostryx); *F*, ground plan of bostryx; *G*, ground plan of cincinnus. *1-9*, successive, relatively main axes. In order to make the relations clearer the successive axes in *A-D* and *F*, *G* are indicated in different colours. The subtending leaf borne by each axis has the same colour as the axis from which it springs. (*A-G*, after EICHLER, the rest modified from KARSTEN.)

B. The median plane of each lateral shoot (of the 1st, 2nd, 3rd order, etc.) is always transverse, *i.e.* right or left of the median plane of the subtending leaf on the parent shoot. Such branch-systems can only be represented in ground plan.

(α) The successive lateral shoots are placed always to the same side, either to the right or the left, BOSTRYX (Fig. 155 *F*).

(β) The successive lateral shoots stand alternately to the right or left, CINCINNUS (Fig. 155 *G*, Fig. 154).

The bostryx and cincinnus are readily understood by deriving them from the ground plan of the dichasium (Fig. 155 *E*).

Various types of branching are frequently combined in one branch-system. Thus cymosely-branched lateral shoots may be borne on the racemose main shoot. The combinations are especially varied in the case of inflorescences.

(b) The Root

The ROOTS of plants, which are usually situated in the soil (subterranean roots) and less commonly exposed to the atmosphere (aerial roots), NEVER BEAR LEAVES. In this respect, as well as by the absence of the green colour, their appearance differs from that of shoots; even of colourless subterranean shoots. Their chief functions are to attach the plant to the soil and to absorb from this water and salts that are conducted to the shoot-system. The functions of roots are thus very different from those of most shoots, which mainly serve for the assimilation of carbon dioxide.

1. **Growing Point.**—The root grows in length at the tip, exhibiting APICAL GROWTH by means of its conical GROWING POINT. The latter requires to have the thin-walled meristematic cells specially protected since, as the root grows, it is forced forwards like a needle between the angular particles of the soil. This protection is afforded by a special organ composed of permanent tissue which is called the ROOT-CAP or CALYPTRA; it covers the tip of the root as a thimble does that of the finger, the true growing point having an intercalary position within the tissue of the root-tip. The outer cell walls of the root-cap become mucilaginous, and this makes the forward passage of the root easier. The root-cap is usually only recognisable in median longitudinal sections through the root-tip (Figs. 156, 157), but in some cases (*Pandanus*) the cap is to be clearly seen on the intact root.

The very noticeable caps on the water roots of Duckweed (*Lemna*) and of some Hydrocharitaceae are not really root-caps, as they are not derived from the root, but from a sheath which envelops the rudimentary root at the time of its origin. They are accordingly termed ROOT-POCKETS. As a general rule, however, roots without root-caps are of rare occurrence, and in the case of the Duckweed the root-pocket performs all the functions of a root-cap. The short-lived root of the Dodder (p. 190) affords another example of a root devoid of a root-cap.

The growing point of the root, as has been already mentioned, is composed of meristematic cells from which the permanent cells of the root-cap are derived on the side towards the tip and the permanent tissue of the root on the basal side.

In most Pteridophytes the root, like the shoot, has a three-sided apical cell (*t*, Fig. 156) with the form of a three-sided pyramid.

In addition to the segments cut off parallel to the three inner walls which contribute to the root itself, segments are formed parallel to the outer wall (*k*). These undergo further divisions and form the root-cap.

The growing points of the roots of Phanerogams, on the other hand, have no apical cells. They consist of equivalent meristematic cells that are frequently arranged in regular layers.

The apex of a root of one of the Gramineae (Fig. 157) may be described as an example. The stratified meristem, from which the permanent tissue of the root arises, is separated into an outer layer of cells, the DERMATOGEN (*d*); a central region formed of several layers which gives rise to the central cylinder of the root and is called the PLEROME (*pl*); and into a number of layers between the derma-

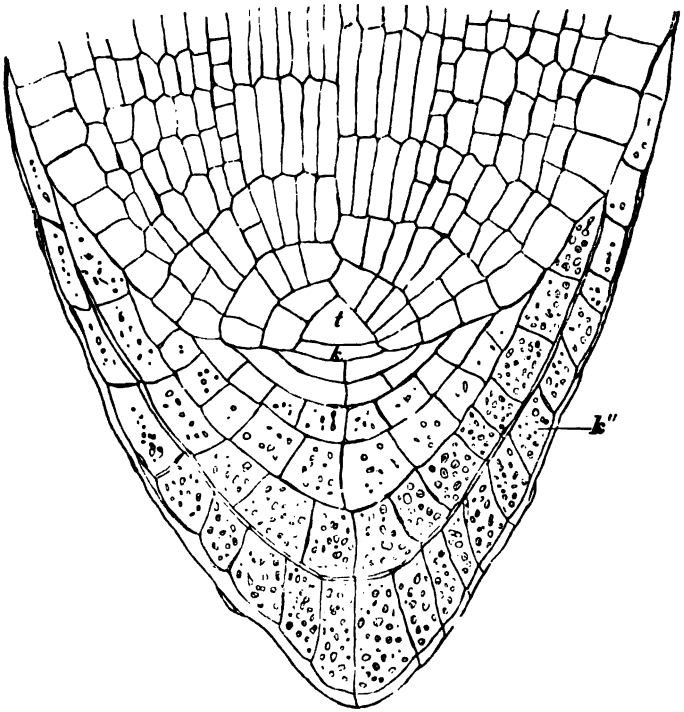


FIG. 156.—Median longitudinal section of the apex of a root of *Pteris cretica*. *t*, Apical cell; *k*, initial cell of root-cap; *k''*, root-cap. (× 240. After STRASBURGER.)

togen and plerome which form the PERIBLEM. The dermatogen (*d*) and periblem (*pr*) unite at the apex in a single cell-layer, outside of which lies the CALYPTROGEN (*k*) or layer of cells from which the root-cap takes its origin.

In many other roots, however (in the majority of Dicotyledons), the formation of the root-cap results from the periclinal division of the dermatogen itself, which, in that case, remains distinct from the periblem. In Gymnosperms, and in many Leguminosae, the dermatogen, periblem, and calyptrogen are not marked out as distinct regions. In roots, the plerome cylinder (*pl*) almost always terminates in special initial cells.

2. External Features of the Root.—Behind the growing point

the meristematic cells enlarge greatly as they are transformed into permanent tissue, a marked elongation of the root accompanying these processes. By this growth in length, which begins close behind the

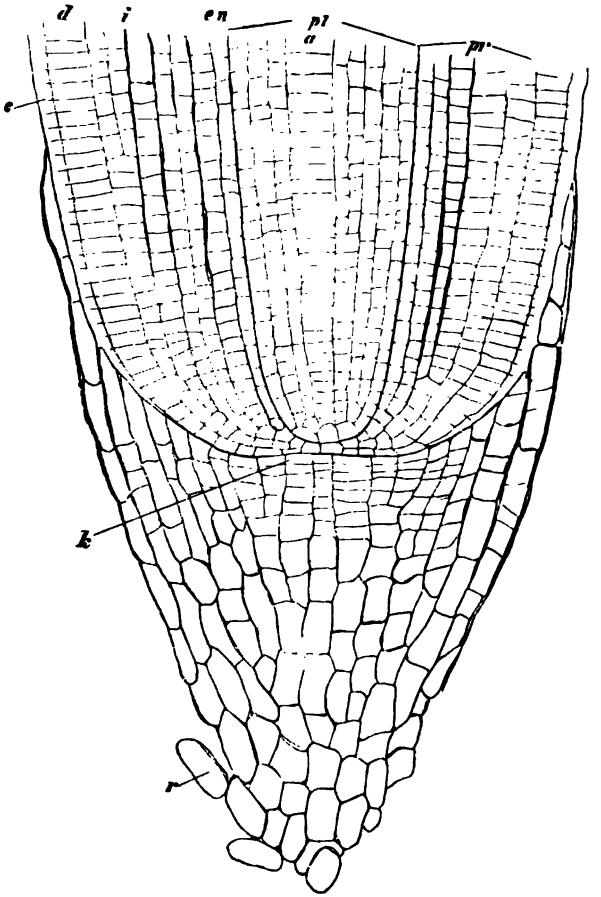


FIG. 157.—Median longitudinal section of the apex of a root of the Barley, *Hordeum vulgare*. *k*, Calyptrogen; *d*, dermatogen; *c*, its thickened wall; *pr*, periblem; *pl*, plerome; *en*, endodermis; *i*, intercellular air-space in process of formation; *a*, cell row destined to form a vessel; *r*, exfoliated cells of the root-cap. (× 180. After STRASBURGER.)

apex and in subterranean roots is limited to a zone only 5-10 mm. long, the root becomes a cylindrical colourless structure.

In the shortness of the zone of elongation subterranean roots contrast with aerial shoots. In aerial roots this zone may be many centimetres in length. Its shortness in subterranean roots is evidently connected with the conditions of their life.

At some distance from the root-tip, about the region where growth

in length ceases, the ROOT-HAIRS (69) (Fig. 158 *r*, Fig. 51), which are important appendages of subterranean roots, appear. They are localised tubular protrusions of the living epidermal cells with thin walls covered with mucilage. When seedlings, *e.g.*, of Wheat are grown in a moist chamber they can be seen with the naked eye, forming a delicate down on the surface of the root. They occur in enormous numbers (*e.g.* about 420 per sq. mm. in *Zea Mays*). Their length varies, according to the kind of plant, between 0·15 and 8 mm. They enlarge the surface of the root greatly (in *Pisum*, for example, twelvefold) and penetrate between the particles of the soil and become attached to them. Thus in the soil they do not retain the cylindrical form seen in moist air but are bent to and fro, and flattened, club-shaped, or lobed at the top (Fig. 239). They serve to absorb water and dissolved salts. They only live for some days, the older root-hairs dying off as new ones form nearer the tip; thus only a limited zone of the young root some centimetres or millimetres in length is clothed with them. The older smooth portion of the root serves for conduction, but has ceased to absorb the water. The surface often shows transverse wrinkling brought about by subsequent contraction of this region of the root. This shortens the root so that, like a tense support, it anchors the shoot more firmly in the soil (cf. Fig. 207, 6).

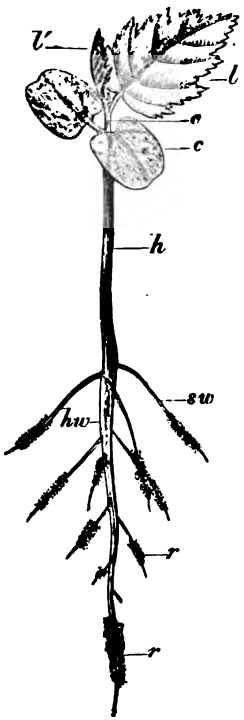


FIG. 158.—Seedling of *Carpinus Betulus*. *r*, Zone of root-hairs near root-tip; *h*, hypocotyl; *hw*, main root; *sw*, lateral roots; *l*, *l'*, leaf; *e*, epicotyl; *c*, cotyledons. (Nat. size. After NOLL.)

Root-hairs are wanting in some plants, especially those which can readily obtain water, as is the case with many aquatic and marsh plants. The roots of some aquatic plants, such as *Nuphar luteum*, form root-hairs when they penetrate the soil; the roots of marsh plants, such as *Carex paludosa*, when there is lack of water.

3. Primary Structure of the Root.—When the transformation of the meristematic cells into permanent tissue has taken place the same kinds of tissue are recognisable in roots as in shoots, their arrangement being as a rule radially symmetrical.

The surface of the younger portions of the root is bounded by the thin-walled EPIDERMIS which, with the root-hairs borne upon it, serves for absorption. The ABSENCE OF STOMATA and of a CUTICLE is characteristic of this layer. The epidermis of the root dies off with

the root-hairs. The outermost layer of the cortex then forms a cutis-tissue called the EXODERMIS ([70]) on the surface, the cell walls becoming more or less suberised (Fig. 159 *ex*).

Some of the cells of the exodermis often remain unsuberised and serve as transfusion cells. They are regularly placed among the corky cells and smaller than the latter.

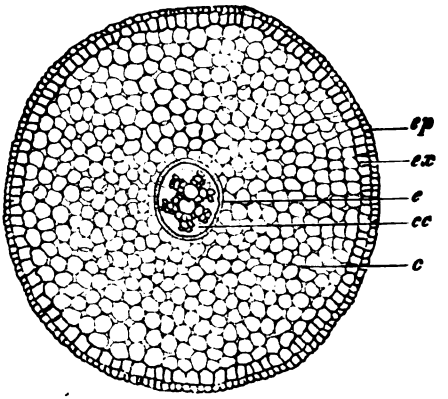


FIG. 159.—Transverse section of an adventitious root of *Allium Cepa*. *ep*, Remains of the epidermis; *ex*, exodermis; *c*, primary cortex; *e*, endodermis; *cc*, central cylinder. (× 45. After M. KOERNICKE.)

The remaining tissues of the root can be distinguished into cortex and central cylinder.

The primary cortex of the root is composed of colourless tissue, which is usually parenchymatous. In the outer layers the cells are in close contact with one another, but intercellular spaces are present more internally. These intercellular spaces often widen into air-cavities or passages. In many roots a hypoderma giving mechanical support to the epidermis or exodermis is present. The innermost layer of the cortex is usually developed as an ENDODERMIS ([71]) (Figs. 159, 160 *e*, 161 *S*, 163 *s*), which sharply marks the limit between cortex and central cylinder. The endodermis consists of somewhat elongated, rectangular, prismatic cells which in transverse sections show the dark Caspary dots on their radial walls. The nature of these strips of the wall (cf. p. 58) shuts off to some extent the central cylinder from the primary cortex; the tangential walls of the young endodermal cells, however, allow of passage of water between the two regions.

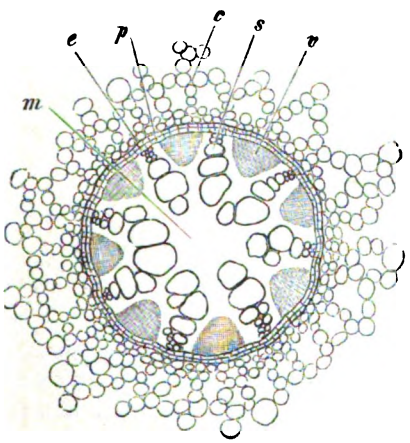


FIG. 160.—Transverse section of central portion of the root of *Acorus Calamus*. *m*, Medulla; *s*, xylem; *v*, phloem; *p*, pericycle; *e*, endodermis; *c*, cortex. (× 90. After STRASBURGER.)

In the older parts of the roots the cells of the endodermis become corky, and in many Monocotyledons are greatly thickened, but generally on one side only.

Should thickening occur at an early stage, special endodermal cells, directly external to the xylem strands, remain unthickened and serve as TRANSFUSION CELLS (Fig. 163 *d*).

The outermost layer of cells of the central cylinder lying immediately within the endodermis (Figs. 160 *p*, 161 *pc*, 163 *p*) forms the PERICYCLE; this is usually a single layer and in rare cases is wanting. The strands of xylem and phloem run longitudinally in the central cylinder and in all roots form a radial vascular bundle (59) (cf. p. 99). They are separated from one another by one or more

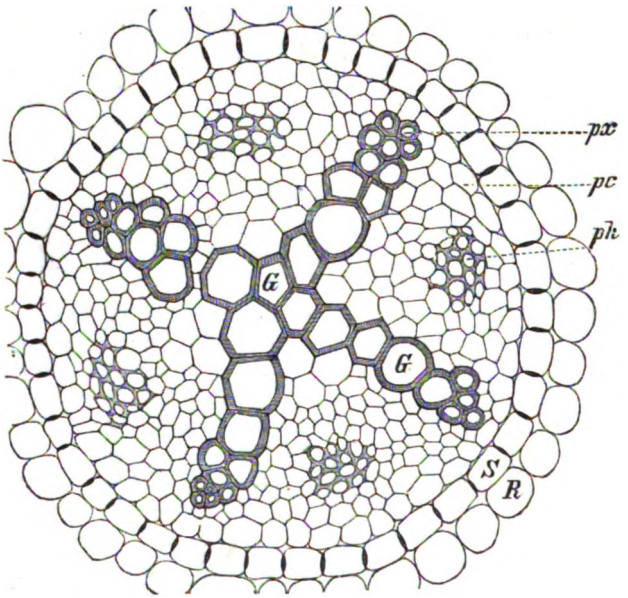


FIG. 161.—Transverse section of the radial bundle of the root of *Ranunculus acer*. *R*, Cortical parenchyma; *S*, endodermis; *pc*, pericycle; *ph*, phloem; *px*, protoxylem; *G*, pitted vessels. (× 200. ROTHERT modified from DIPPEL.)

layers of cells that usually have the characters of conducting parenchyma. The orientation of the strands of xylem in the root contrasts with that found in the stem. In the stem the narrow elements of protoxylem were situated internally, but in the root the internal vessels are the widest, and the narrow elements of the protoxylem are found close to the periphery of the vascular bundle. Annular, spiral, reticulate, and pitted vessels thus follow in order from without inwards. The protophloem is situated at the outer margin of the phloem strands, which are more or less circular in cross-section. Roots are described as diarch, triarch, polyarch, etc, according to the number of the vascular strands. Thus the root in Fig. 160 is octarch

and that in Fig. 163 pentarch. The vascular strands may either meet in the centre (Figs. 161, 163) or there is in this position a central strand composed of parenchyma or sclerenchyma or a mixture of these tissues (Fig. 160). Most roots have to be constructed to resist pulling strains, and the mechanical tissue is accordingly mainly placed compactly in the central pith (Fig. 162).

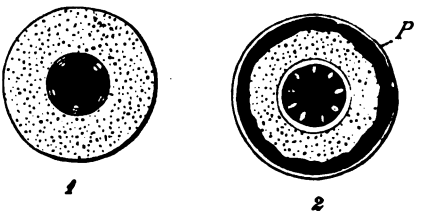


FIG. 162.—Mechanical tissue of roots. *1*, Centrally placed to resist longitudinal pulling strains; *2*, a prop root with a peripheral layer of mechanical tissue (*P*) to resist lateral pressure, in addition to the central strand. (After NOLL.)

For an organ that has to resist tension it is immaterial at what part of the cross-section the mechanical tissues are placed. Their association in the centre to form a single strand is of advantage, since, if many thinner strands were situated peripherally, a one-sided pull might rupture some of these more readily.

The continuity of the xylem and phloem strands of the radial bundle of

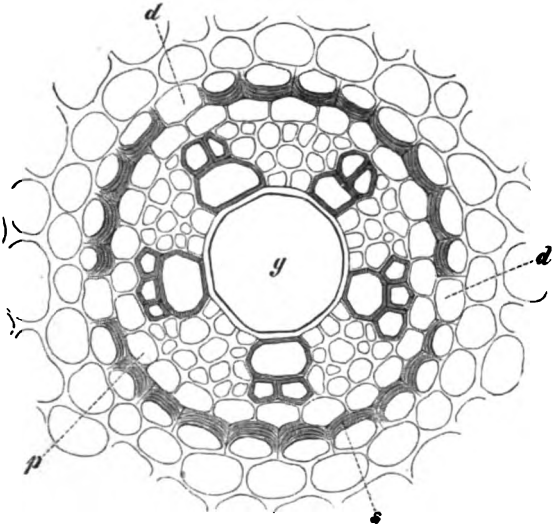


FIG. 163.—Transverse section of the radial bundle of the root of *Allium ascalonicum*. *s*, Endodermis with the inner walls thickened; *d*, transfusion cells; *p*, pericycle; *g*, large central vessel. (ROTHERT after HABERLANDT.)

the root with the corresponding tissues of the differently-constructed bundles of the stem is effected at the junction of the root and stem of the seedling. It need only be briefly described for the most common case of plants in which the bundles of the stem are collateral. The essential fact of the transition

is that each of the strands of xylem of the root rotates through 180° round its longitudinal axis, bringing the protoxylem to the inner side of the strand which is the characteristic position in the stem. A number of collateral vascular bundles are reconstituted from the tissues of the radial bundle of the root by the radially-arranged xylem and phloem taking up the collateral position. This happens in different ways, of which two main types may be distinguished: 1. The strands of xylem when rotating follow a straight course from the root to the stem; the strands of phloem of the root, on the other hand, divide radially, the two halves separate tangentially, and, uniting with the portions derived from adjoining strands of phloem, come to lie outside the xylem strands. 2. The phloem strands of the root follow a straight course into the stem, but the strands of xylem which rotate through 180° split radially; the halves separate tangentially (as the phloem strands did in Type 1) and, uniting with the portions derived from the adjoining strands of xylem, place themselves internal to the strands of phloem to constitute the collateral bundles.

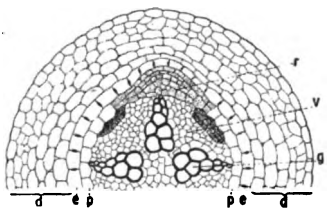


FIG. 164.—Transverse section of the root of *Vicia Faba* showing the origin of a lateral root (*r*). *e*, Endodermis; *p*, pericycle; *d*, cortex; *g*, xylem strand; *v*, phloem strand of the radial bundle. (× 40. Somewhat diagrammatic.)

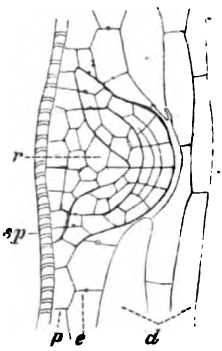


FIG. 165.—Portion of a longitudinal section of a root of *Amarantus* showing the origin of a lateral root. *e*, Endodermis, already absorbed opposite the young root; *d*, cortex; *p*, pericycle; *sp*, spiral tracheide; *r*, young lateral root. (× about 200. After PH. VAN TIEGHEM.)

4. Branching of the Root.—By this process, in which a root always gives rise to roots, the root-system can penetrate the soil in all directions and obtain from the whole space thus occupied water and dissolved salts.

DICHOTOMOUS branching by an equal division of the growing point only occurs in some Pteridophyta (Lycopodinae).

With this exception the branching of the root is LATERAL (Fig. 158), the lateral roots, in contrast to the lateral shoots, originating at some distance from the growing point where the meristematic cells have been transformed into permanent tissue. They arise ENDOGENOUSLY (Figs. 164, 165) within the tissues of the parent root and in acropetal succession. The growing point of the new root is formed from the innermost layer of the cortex in Pteridophytes and from the pericycle in the Phanerogams; a group of parenchymatous cells commences to divide, the cells returning to the meristematic condition.

The lateral roots break through the whole thickness of the cortex as they emerge in the order of their development from the main root. The ruptured cortex is frequently recognisable as a sort of collar round the base of the lateral root. Other lateral roots may form subsequently between those already developed and on older parts of the root.

The lateral roots always stand in VERTICAL SERIES on the parent root ([72]). This arrangement is determined by their always arising either opposite one of the longitudinally-running strands of xylem (Fig. 164), or opposite the plate of conducting parenchyma which separates a strand of xylem from one of phloem. The number of vertical series of roots is thus either the same as the number of strands of xylem, or twice this. In the former case the lateral distance between any two adjacent roots is equal, while when the roots arise right and left of a strand of xylem these two vertical rows are approximated.

The structure of the lateral roots corresponds with that of the main root, and the xylem and phloem are continuous from the one to the other.

5. Roots borne on Shoots.—Roots not only arise from other roots but may be developed from the shoot, both from stems and leaves. They are usually endogenous. In Ferns they arise from meristematic tissue in the region of the growing point of the shoot.

The place of origin of such adventitious roots is not fixed beforehand but may be more or less definite. This is especially the case in marsh and water plants where the roots arise from the lower nodes of the stem between, and alternating with, the leaves; they replace the primary root-system which has been lost when the older part of the plant died off ([73]). They are especially numerous on the under side of rhizomes (Fig. 138) and creeping shoots. A young shoot, or a cutting planted in moist soil, quickly forms adventitious roots, and roots may also arise in a similar manner from the bases of leaves, especially from *Begonia* leaves when planted in soil ([74]).

Dormant root-rudiments occur in the same manner as dormant buds of shoots. Willow-twigs afford a special case of the presence of such dormant rudiments of adventitious roots, the further development of which is easily induced by darkness and moisture.

6. Appearance of the Root-System. — The lateral roots of successively higher orders are as a rule thinner and grow less strongly than their respective parent roots. The whole root-system is thus typically RACEMOSE. The alternate branches are usually short and have a limited period of existence; they may be termed ABSORBENT ROOTLETS.

The root-system, like the shoot-system, further owes its general appearance to the fact that the main and lateral branches take up distinct positions in space relatively to one another; this depends on differences in their geotropism (cf. p. 339).

Many Dicotyledons (*e.g.* Lupin, Oak) and Gymnosperms (Pine) possess a radial MAIN-ROOT or TAP-ROOT (Fig. 158) which, from the seedling onwards, forms the downward continuation of the main stem and grows vertically down into the soil (orthotropous). On this radial lateral roots of the 1st order arise, which penetrate the soil horizontally or obliquely (plagiotropous). The lateral roots of the 2nd order arise in turn on those of the 1st order. They tend to grow on all sides from the latter so that the branches of the root-system penetrate the soil as uniformly as possible in all directions, and, as branching continues, do not leave a cubic centimetre unused.

A tap-root is usually wanting in Monocotyledons since it becomes arrested in the seedling stage. In its place numerous roots arise from the base of the stem and penetrate the soil vertically, obliquely, or horizontally. They branch monopodially, bearing lateral roots of successively higher orders which penetrate the soil in all directions. In the Wheat, for example, there is no tap-root, but the root-system continues to extend in a horizontal plane.

The length of all the roots of a plant taken together is surprising. Thus for a plant of Wheat it may amount to some hundreds of metres.

Some of the roots of trees in tropical forests are developed in a peculiar fashion. The extraordinarily high and thick stems of many such trees are supported at the base by strong vertically-placed BUTTRESS-ROOTS. In other cases support is given by aerial roots growing down from the branches to the earth and attaining the thickness of woody trunks (PROP-ROOTS, *e.g.*, in species of *Ficus*).

(c) Secondary Growth in Thickness of the Cormus

It has been seen that the additions to the root and shoot made by the increase in number of the meristematic cells in the growing points increase in length as they mature. A certain increase in thickness of the parts is associated with this growth in length; this depends on the enlargement of the cells on passing from the meristematic condition and not on increase in their number (PRIMARY GROWTH IN THICKNESS, cf. Figs. 98, 100, 102, 115). This, as a matter of fact, is slight, but is often followed in stems and roots by processes of growth that will now be considered.

The larger the shoot-system becomes the more readily will it escape overshadowing by other plants and form more organic material. Thus in many plants the growth of the small seedling with a few leaves leads, with the accompanying branching, to a cormus of the size of a large tree bearing a very large number of leaves. The increase in the aerial shoot-system and in the number of leaves makes progressively great demands on the water supply from the roots, which can only be met by the increase of surface and the branching of the root-system; in many cases additional roots are

developed from the stem. All increase of the root-system, however, depends on a supply of organic food materials manufactured in the leaves. Thus the further development of the crown of foliage and of the root-system are intimately related to one another. The increase in size of the shoot- and root-systems further presupposes that a sufficient number of conducting tracts in the stems and roots can be developed, both for water and for organic materials, and that the stem should be strong enough to support the increasing weight even when exposed to wind. There is thus an intimate connection between the size of the cormus and the formation of conducting tracts in its axes and the rigidity of the shoot.

The rigidity requires to be greater the larger the plant becomes and the longer it lives. Plants or shoot-systems which only live for a limited period and die off after bearing reproductive organs have usually herbaceous structure (HERBS). Large cormi which live for many years and bear fruit repeatedly have as a rule the rigidity of their stems and roots increased by the formation of wood. Such woody plants are called SHRUBS if they do not exceed a moderate height, and retain their lateral shoots so that their branches are formed near the ground. They are called TREES (75), on the other hand, if they attain a greater height, have a main stem or trunk (which must have the type of rigidity possessed by a pillar), and usually lose their lower branches at an early period.

In catalogues and descriptions of plants the duration of the period of growth is usually expressed by special symbols: thus ☉ indicates an annual; ☉ a biennial, and ♃ a perennial herb; ♄ is employed to designate shrubs, and for trees the sign ♄ is in use. A special type of tree is found in the columnar and usually unbranched stems of Palms and Tree-ferns; in them secondary thickening, and a true woody mass resulting from this, are wanting.

The requirements, both as regards the number of conducting tracts and the necessary rigidity, are met in a variety of ways in cormophytic plants. In the first place, there are plants in which the main axis of the seedling and any lateral branches that arise attain a sufficient thickness and develop sufficient mechanical and conducting tissues before growth in length; when this takes place later the thickness is adequate for the future increase in size of the plant. The primary root in such cases remains thin and usually dies off early, while as many roots as are necessary arise from the basal portion of the shoot. Secondly, there are plants in which long slender stems and roots with only a few conducting and mechanical elements are first developed. A limit would soon be set to the supply of water to the leaves and of nutritive material to the root-system, and thus to the increase in size of the plant, by the small number of conducting elements in the primary stem and root. Provision is, however, made for an increase in the conducting and mechanical

tissues corresponding to the needs of the growing plant. This is effected by a continued process of cell division forming secondary tissues and leading to a SECONDARY GROWTH IN THICKNESS of the stem and roots. Secondary tissues are those that are added to or replace the primary tissues as a result of the activity of a secondary meristem or CAMBIUM (cf. p. 47). Such secondary growth occurs in herbaceous as well as in woody plants.

To the FIRST TYPE ([76]) belong the mostly herbaceous Pteridophytes and Monocotyledons, including nearly all the forms that have definite stems (Tree-ferns, Palms, Pandanaceae, certain Liliiflorae). Thus in these stem-forming Monocotyledons the embryonic stem remains very short on germination. The primary meristem of the flattened growing point increases in breadth, leading to the axis of the seedling from which the stem will continue having a considerable thickness from an early stage.

In such forms as the Palms and Pandanaceae the stem may continue to increase slightly in thickness after the permanent tissues have developed by a process of expansion of the cells. The cells of the sclerenchymatous strands which accompany the phloem of the vascular bundles may thus increase in diameter leading to an enlargement of the strand as a whole. In places this growth in thickness may be accompanied by divisions in parenchymatous cells (*e.g.* in some Palms).

The majority of herbaceous and woody Gymnosperms and Dicotyledons and some arborescent Liliiflorae belong to the SECOND TYPE ([77]). The primary thickening or maturing of the stem and root dependent on the enlargement of cells is in them followed by increase in number of the cells in a special meristematic zone, the cambial ring.

The secondary thickening in annual, scrambling, and twining plants often only begins in older internodes which have long attained their full primary size. In the twigs of trees, on the other hand, the secondary growth may start early, even before the primary tissues are fully developed.

Secondary growth in thickness was present in certain Pteridophytes known to us as fossil remains, but only became of general occurrence in the Gymnosperms and Dicotyledons.

Secondary Growth in Thickness of Monocotyledons.—In some arborescent Liliiflorae (*Dracaena*, *Cordyline*, *Yucca*, *Aloe*) the axis exhibits growth in thickness due to a secondary meristem. This arises in the cortex where it abuts on the central cylinder in which the vascular bundles are scattered in the manner characteristic of Monocotyledons. In transverse sections divisions can be seen to begin in an annular zone of mature cortical cells. In *Dracaena* this happens at a considerable distance from the growing point, but in other cases it may start close to it. A cylindrical meristematic zone a number of cells deep is thus formed; the cells are prismatic and fit together without intercellular spaces. As a result of the formation of

tangential walls, cells continue to be cut off towards the inside, and later some are formed to the outside. The latter become secondary cortical tissue; the cells to the inside develop into concentric vascular bundles, in which the xylem surrounds the phloem, and parenchymatous tissue with thickened and lignified walls (Fig. 166).

The meristematic cells have a rectangular shape in transverse and radial sections, while in tangential section they are polygonal; they are thus tangentially-placed flattened prisms (cf. Fig. 169 *A*, *II*). So long as the meristem is only forming new tissues on the one side, the initial cells can be replaced at the expense of the inner permanent cells of the cortex. When, however, the meristem is active on both sides the initial layer persists.

True secondary thickening of the root in Monocotyledons is only known in the case of the genus *Dracaena*. The cambial ring arises in the cortex of the root just outside the endodermis.

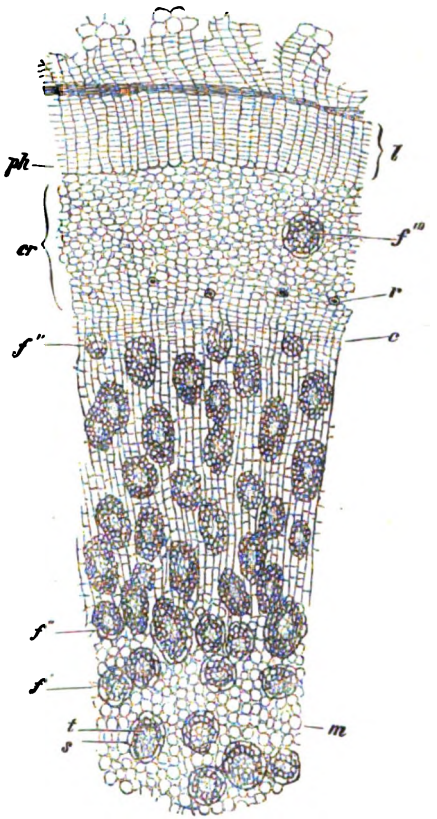


FIG. 166.—Transverse section of the stem of *Cordyline* (*Dracaena*) *rubra*. *f*, Primary vascular bundles; *f''*, secondary vascular bundles; *f'''*, leaf-trace bundle within the primary cortex; *m*, parenchymatous fundamental tissue; *s*, bundle-sheath; *t*, tracheides; *c*, cambium ring; *cr*, cortex, the outer portion being primary, the inner secondary cortex; *ph*, cork cambium; *l*, cork; *r*, bundles of raphides. (× 30. After STRASBURGER.)

Secondary Thickening of Gymnosperms and Dicotyledons. 1. Formation, Structure, and Activity of the Cambium in Stems.—In the open vascular bundles of the Gymnosperms and Dicotyledons the formation of secondary tissues may take place as soon as the primary tissues have matured, or may even begin before this. Only the former case need be considered here. The primary meristem remaining between the xylem and phloem of the bundle becomes the cambium and commences again to divide actively. The vascular bundles are usually arranged in a circle. When the cambial activity has commenced in the bundles, cambium also forms across the medullary rays, by parenchymatous cells dividing tangentially. This

INTERFASCICULAR CAMBIUM connects the FASCICULAR CAMBIUM within the bundles, forming a complete hollow cylinder of meristematic tissue. The cells grow in the radial direction and undergo division by tangential and by transverse walls; from time to time cells appear to be divided by radial walls.

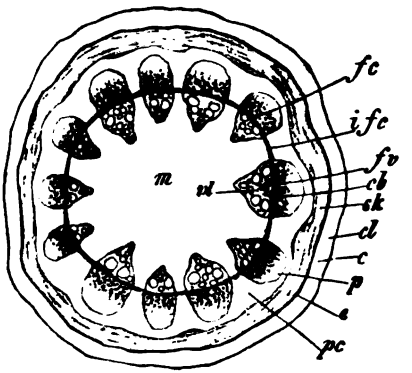


FIG. 167.—Transverse section of a stem of *Aristolochia Sipho* 5 mm. in thickness. *m*, Medulla; *fv*, vascular bundle; *xl*, xylem; *cb*, phloem; *fc*, fascicular cambium; *ifc*, interfascicular cambium; *p*, phloem parenchyma; *pc*, pericycle; *sk*, ring of sclerenchyma; *e*, starch-sheath; *c*, primary cortex; *cl*, collenchyma in primary cortex. (× 9. After STRASBURGER.)

Figs. 167 and 168 represent the formation of the cambium as shown particularly clearly and simply in a transverse section of the stem of *Aristolochia Sipho*. A single bundle with the adjacent interfascicular cambium from the stem in Fig. 167 is more highly magnified in Fig. 168. The cambium is actively dividing, and two partially-developed secondary vessels are seen at *m''*. The outline of the parenchymatous cells of the medullary rays, which gave origin to the interfascicular cambium, can still be recognised.

The cambium cells fit together without intercellular spaces and form radial rows. They have the shape of elongated prisms more or less flattened tangentially and with both ends pointed; thus the form of the cell appears very different in tangential, radial, or transverse section (Fig. 169). The tangential walls, which form the polygonal or rhombic main faces of the prismatic cell, are thin; the radial walls, on the other hand, are fairly thick and frequently pitted. A middle layer of cells in the cambial zone forms the INITIAL LAYER. Its cells remain permanently in the meristematic condition. They grow in the radial direction, dividing by tangential walls, and so give off daughter cells (tissue mother cells) to both sides, but more abundantly on the inner side. These daughter cells in their turn may undergo tangential divisions, and, often after growing greatly in length and breadth (Fig. 174) and changing their shape, become gradually transformed into permanent cells of the secondary tissues.

The cambium in giving off cells inwards must itself, as the stem grows in thickness, be carried gradually outwards. The circumference of the cambial ring must therefore be increased. This can only be effected by growth and increase in number of the cells in a tangential direction. In transverse sections it appears as if this came about by radial division of some of the cells. KLINKEN [78] has, however, shown in *Taxus* that such divisions do not occur; the number of cells in the tangential direction is increased by an initial cell of the cambium dividing transversely, and the ends of the two resulting cells becoming placed side by side tangentially by sliding growth.

All the permanent tissue formed on the inner side of the cambium is termed wood; this is usually hard and composed of more or less lignified cells. The tissue formed to the outside by the cambium usually consists of unlignified cells and is termed the bast.

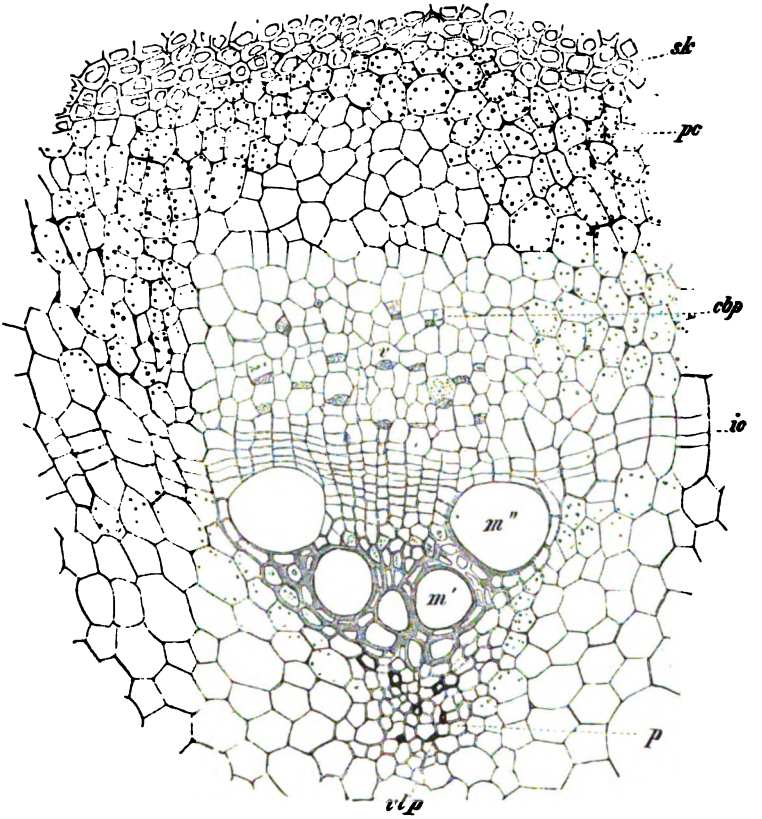


FIG. 168.—Transverse section of a stem of *Aristolochia Sipho* in the first year of its growth, showing a vascular bundle with cambium in active division. *p*, Xylem parenchyma; *vlp*, protoxylem; *m'* and *m''*, vessels with bordered pits; *ic*, interfascicular cambium in continuation with the fascicular cambium; *v*, sieve-tubes; *cbp*, protophloem; *pc*, pericycle; *sk*, inner part of ring of sclerenchymatous fibres. (× 130. After STRASBURGER.)

In contrast to the primary cortex all the tissues to the outside of the cambium may be regarded as forming secondary cortex.

The secondary tissue formed internally by the fascicular cambium resembles the xylem, and that to the outside the phloem of the primary vascular bundle. By the activity of the interfascicular cambium the primary medullary rays are continued through the wood and the bast. Their breadth is, however, usually diminished, since

the interfascicular cambium in great part gives rise to tissues similar to those formed by the fascicular cambium. Thus, in place of the original broad medullary rays, the cambium forms at definite points narrower radial rows of medullary ray tissue. These medullary rays, which are spindle-shaped when cut across (Fig. 170), traverse the wood and the bast, connecting the pith with the cortex as PRIMARY MEDULLARY RAYS. As the thickness of the secondary wood and bast increases, SECONDARY MEDULLARY RAYS are developed from the fascicular cambium. In one direction the secondary medullary rays

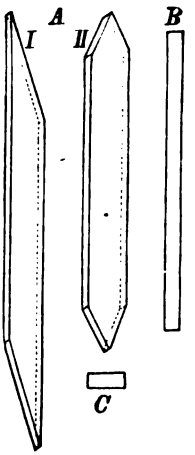


FIG. 169.—Diagrammatic figure of the shape of cambial cells. *A*, *I* and *II*, the two forms which occur, seen from the tangential face; *B*, in radial section; *C*, in transverse section. (After ROTHERT.)

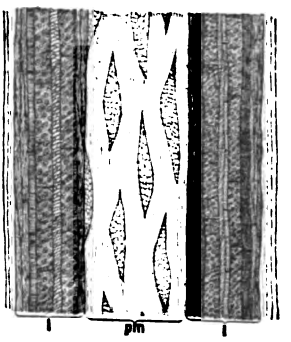


FIG. 170.—A diagrammatic tangential section to illustrate the subdivision of a primary medullary ray into many smaller rays on the commencement of secondary thickening. *l*, *l*, Adjoining primary vascular bundles; *pm*, primary medullary ray transformed by the activity of the interfascicular cambium into many small spindle-shaped medullary rays and reticulately-connected secondary vascular bundles.

end blindly in the wood and in the other in the bast; the later they develop the less deeply do they penetrate the tissues on either side of the cambium (Fig. 179).

The cambial cells which give rise to medullary rays are shorter and their end walls are more horizontal, for when a medullary ray is to be initiated the ordinary cambium cell becomes divided transversely or obliquely.

The origin of the cambium and the nature of its activity can be distinguished into three main types according to the primary construction of the stem: 1. The stem has a circle of collateral vascular bundles separated from one another by broad medullary rays; the breadth of the medullary rays is maintained during secondary growth, the interfascicular cambium producing only medullary ray tissue. This is the case for many herbaceous plants, but among

woody plants is only found in the lianes. In those herbs in which the inner portion of the medullary rays between the primary strands of xylem consists of sclerenchyma (cf. p. 95), the interfascicular cambium forms similar tissue on its inner side. 2. The stem as in the first type has a circle of collateral leaf-trace bundles separated by broad medullary rays. Before the primary growth in thickness is completed there arise from the still meristematic tissue of each medullary ray, that now assumes the characters of a cambium, one or a number of small, cauline, intermediate bundles which anastomose tangentially; the intervening meshes are occupied by narrow primary medullary rays that are spindle-shaped when cut across (Fig. 170). The original medullary rays become filled up in this way in many herbaceous and woody plants. 3. In the transformation of the primary meristem to permanent tissue there arises, instead of a circle of collateral bundles, a vascular tube, which appears like a concentric bundle with a central pith and internally-situated xylem. There is a layer of meristematic tissue between the xylem and phloem that later becomes the cambium. The vascular tube may be traversed by very narrow spindle-shaped primary medullary rays, or these may be completely wanting. This type is found in many trees.

The primary xylem of the bundles in stems which have undergone secondary thickening projects into the pith.

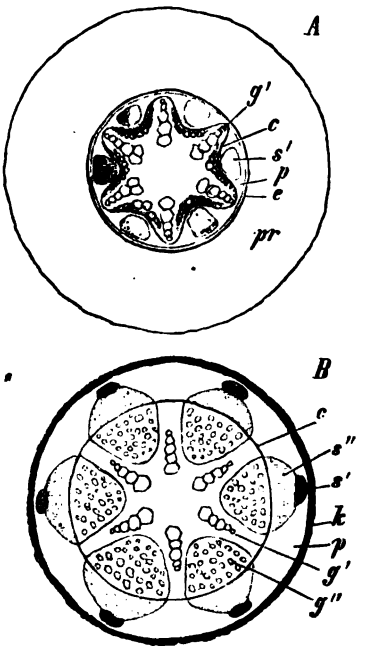


FIG. 171.—Diagrammatic representation of the growth in thickness of a dicotyledonous root. *pr*, Primary cortex; *c*, cambium ring; *g'*, primary vascular strand; *s'*, primary phloem strand; *p*, pericycle; *e*, endodermis; *g''*, secondary wood; *s''*, secondary bast; *k*, periderm. (After STRASBURGER.)

2. Formation and Activity of the Cambium in the Root.—As has been seen (Figs. 160, 161), the strands of xylem and phloem alternate in the central cylinder of the root; they are separated by intervening parenchymatous tissue. When secondary thickening begins in such a root cambial layers arise internal to the strands of phloem, and between these and the strands of xylem, by divisions taking place in some of the parenchymatous cells; the cambium forms wood towards the centre and bast towards the outside. These arcs of cambium meet in the pericycle just outside the xylem strands and the cambial ring is completed from the pericycle. The wavy outline of this is shown in Fig. 171 *A*; by the activity of the cambium in producing new tissues the depressions in the ring are soon evened out (Fig. 171 *B*). Primary medullary rays are absent from the wood and bast, but secondary medullary rays

originate as in the stem. In some plants wide parenchymatous rays are formed by the cambium opposite the strands of primary xylem (Fig. 171 *B*). A cross-section of a root in which the secondary growth has continued for some years can scarcely be distinguished from a cross-section of a stem; by careful examination, however, the characteristic strands of primary xylem can be recognised in the centre of the root.

Repeated Formation of Cambium in Stems and Roots.—Deviations from the usual type of secondary growth as found in most Gymnosperms and Dicotyledons are met with in some cases. These anomalous types are characterised by differences in the distribution and in the activity of the cambium.

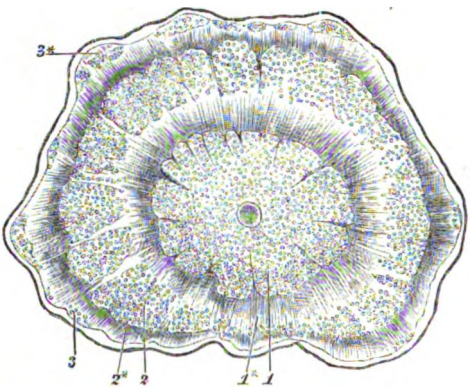


FIG. 172.—Transverse section of the stem of *Mucuna altissima*. *1*, *2*, *3*, Successively-formed zones of wood; *1**, *2**, *3**, successively-formed zones of bast; *3*, *3** are commencing to form within the pericycle. (½ nat. size. After SCHENCK.)

In some Cycadeae and certain species of *Gnetum* among the Gymnosperms and in the Chenopodiaceae, Amarantaceae, Nyctaginaceae, Phytolaccaceae, and some other families of Dicotyledons, the first ring of cambium, which arose in the usual way, ceases to function after a time. A new zone of cambium forms usually in the pericycle, *i.e.* external to the bast, or else in tissue derived from the earlier cambium. The new cambium forms bast externally and wood internally, these tissues being traversed by medullary rays. Its activity in turn comes to an end and its place is taken by a new cambium formed outside this zone of bast. The process can be repeated and leads to the production of concentric zones each composed of wood and bast. This is seen, for example, in the transverse section of the stem of *Mucuna altissima*, a liane belonging to the Papilionaceae which is represented in Fig. 172. Such concentric zones of wood and bast are met with in some succulent roots which persist for two or more vegetative periods. This is the case in the Beet (*Beta vulgaris*), where the zones can be readily recognised with the naked eye on cross-sections. They arise as described above, but, as in the case of the typical secondary growth of other succulent roots, parenchymatous tissue which serves for storage of reserve materials forms a large proportion of the newly-developed tissues.

3. The Wood. A. Kinds of Tissue and their Functions.—The construction of the wood is complex, and in Dicotyledons it is usually composed of three distinct types of tissue the walls of which are more or less lignified. These are: (1) longitudinally-running strands of dead VESSELS (Fig. 173 *g*, *tg*); (2) longitudinally-running strands of sclerenchymatous fibres, WOOD-FIBRES (*h*), that are usually dead; (3) STORAGE

PARENCHYMA (*hp*), which forms longitudinally-running strands, and in the medullary rays is also directed radially; this constitutes the WOOD PARENCHYMA and PARENCHYMA OF THE MEDULLARY RAYS. Corresponding to this the wood serves (1) for water-conduction, (2) to render the stems and roots rigid against pressure and bending, and (3) for the storage of organic materials. The properties which make

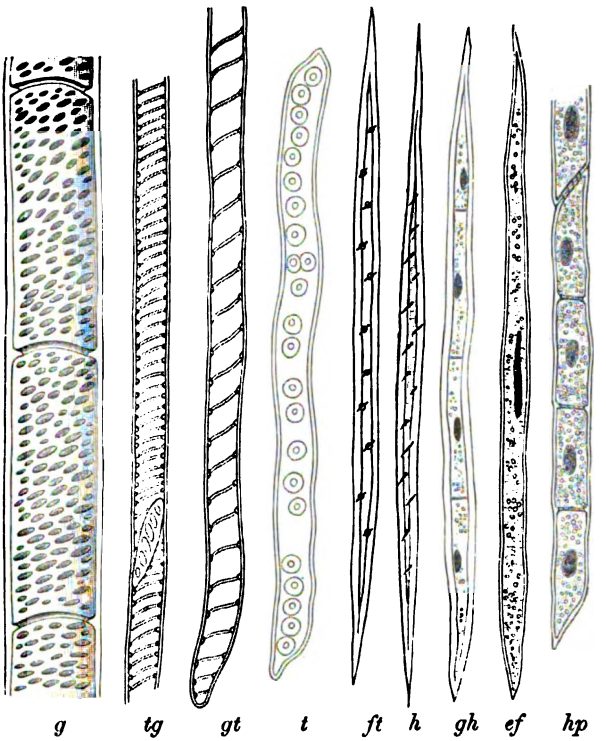


FIG. 173. — Tracheae, tracheides, wood-fibres, and wood parenchyma of a Dicotyledon with transition-forms between the various elements. Diagrammatic. Explanation in text. (Modified after STRASBURGER.)

wood such a valuable building material depend upon its natural function as a mechanical tissue.

The various kinds of cells of which the wood is composed can be most readily studied by treating wood with SCHULTZE's macerating mixture (cf. p. 42).

The vessels are pitted or less commonly reticulately thickened. The tracheae may be wide and composed of short segments, or narrow and formed of more or less elongated cells (Fig. 173 *g*, *tg*); the tracheides are narrow and elongated and serve both for conduction and as mechanical tissue. The wood-fibres (*h*) are usually very long

and narrow, pointed at both ends, and with thick walls provided with narrow oblique pits. The cells of the storage parenchyma (*hp*) are rectangular and prismatic or are spindle-shaped; they are usually elongated in the direction of the long axis and have either thin or thick walls with small, circular, simple pits. They contain abundant reserve materials (starch, oil, or sugar). Intercellular spaces only occur in the parenchymatous strands.

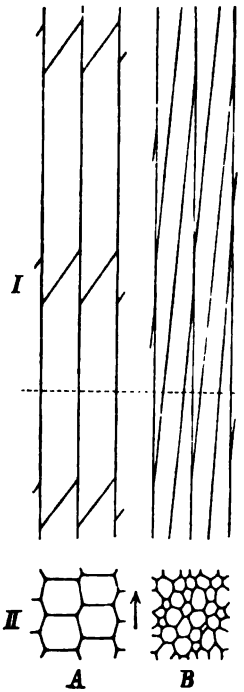


FIG. 174. — Diagrammatic representation of sliding growth, of wood-fibres. *I*, In tangential longitudinal section; *II*, in transverse section along the dotted line in *I*. *A*, *I*, *II*, cells in the young condition; *B*, *I*, *II*, after sliding growth has taken place. (After ROTHERT.)

In many Leguminosae, in the Willow, Poplar, and species of *Ficus*, the water-conducting elements of the wood consists of tracheae only.

The tracheides and wood-fibres are frequently more than 1 mm. in length and are considerably longer than the cambial cells from which they arose. This increased length, like the increased width of the larger tracheae, is attained by sliding growth (p. 48; Fig. 174). In the formation of wood parenchyma the cambial cells undergo repeated transverse divisions. The resulting parenchyma thus consists of rows of cells, the origin of which from a cambial cell is indicated by the row ending above and below in a pointed cell (Fig. 173 *hp*).

The walls between cells of the wood parenchyma or medullary rays and the vessels have bordered pits on the side towards the vessel only, while the larger pits in the living cell have no borders; such pits, in contrast to those bordered on both sides, are characterised by the absence of a torus from the pit membrane. The walls separating vessels and wood-fibres and those between the latter and parenchyma cells are, on the other hand, usually without pits.

In woods composed of vessels, wood-fibres, and parenchyma there are frequently transition forms between the typically-constructed elements, and there is a corresponding lack of sharp distinction as regards function. Narrow tracheae (Fig. 173 *tg*) lead on to the tracheides (Fig. 173 *gt*, *t*). Narrow, sharply-pointed tracheides (fibre tracheides, *ft*), the function of which is mainly mechanical, form the transition to the wood-fibres (*h*). Slightly thickened wood-fibres which retain their living contents (*ef*) and are either without or with transverse walls (*gh*) form the transition to the cells of the wood parenchyma (*hp*).

In the wood of **Gymnosperms** there are only tracheides with typical bordered pits, together with some wood parenchyma and a considerable amount of parenchyma of the medullary rays. The division of labour is here less advanced, the same elements being concerned with the mechanical and water-conducting functions.

Drimys, belonging to the Magnoliaceae, is a Dicotyledon with wood composed of tracheides and parenchyma only.

B. Arrangement of the Tissues in the Wood. — In the **Gymnosperms** (Figs. 175-177) the wood of the stems and roots has thus a relatively simple structure. The tracheides are arranged in regular radial rows (Fig. 175 *A*), in correspondence with their mode of origin. Since they increase in size mainly in the radial direction, and hardly at all in the tangential and longitudinal

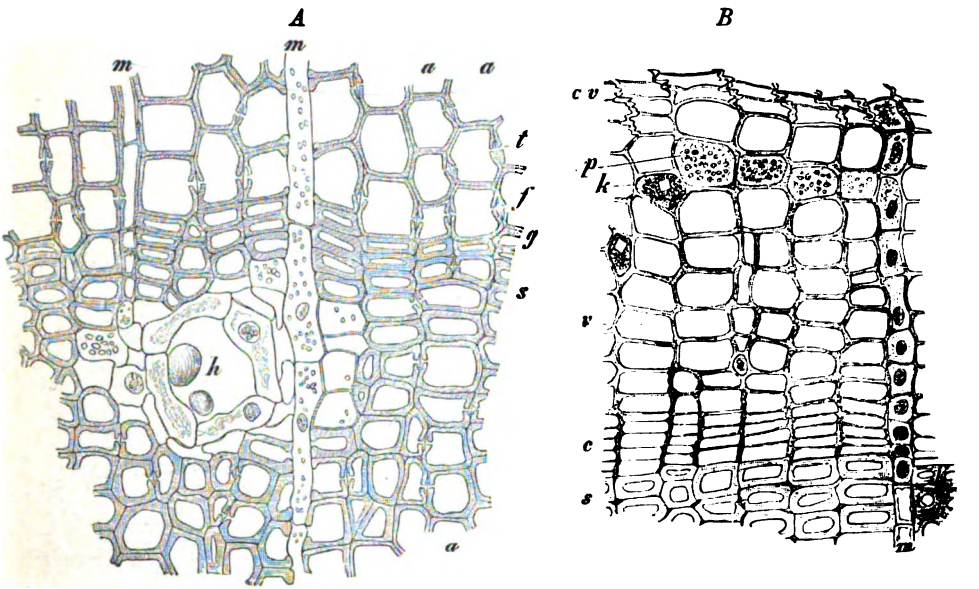


FIG. 175.—*A*, Transverse section of the wood of a Pine at the junction of two annual rings. *f*, Spring wood; *s*, autumn wood; *t*, bordered pit; *a*, interposition of a new row of tracheides; *h*, resin canals; *m*, medullary rays; *g*, limit of autumn wood. (× 240.) *B*, Part of a transverse section of the stem of a Pine. *s*, Late wood; *c*, cambium; *v*, sieve-tubes; *p*, bast parenchyma; *k*, cell of bast parenchyma containing crystal; *cv*, sieve-tubes, compressed and functionless; *m*, medullary ray. (× 240. After SCHENCK.)

directions, they retain the same form as the cambial cells (Fig. 169). They have large, circular, bordered pits frequently only upon their radial walls; the pits are thus seen in surface view in radial sections (Figs. 70 *B*, 71 *A*).

In the wood of most Gymnosperms there is relatively little parenchyma. In the Pines, Firs, and Larches parenchyma is found only around schizogenous resin-canals which run longitudinally in the wood (Figs. 175 *A*, *h*; 179 *h*), and are connected by others which run radially in some of the broader medullary rays. For this reason considerable amounts of resin flow out from the wounded stem of a Pine or Fir. In the other Conifers the wood parenchyma is limited to simple rows of cells, the cavities of which may later become filled with resin.

The medullary rays in the wood of Gymnosperms are numerous, and for the most part only one layer of cells broad (Figs. 175 *m*, 177 *sm*, *tm*; 179 *ms*). Every tracheide abuts in the course of its length upon one or more of these medullary rays. The cells of the medullary ray are elongated in the radial direction; they contain abundant starch and are associated with intercellular spaces (Fig. 177 *i*). They serve to transfer the products of assimilation, formed in the leaves and conducted downwards in the bast, in a radial direction into the wood of the stem or root, where storage takes

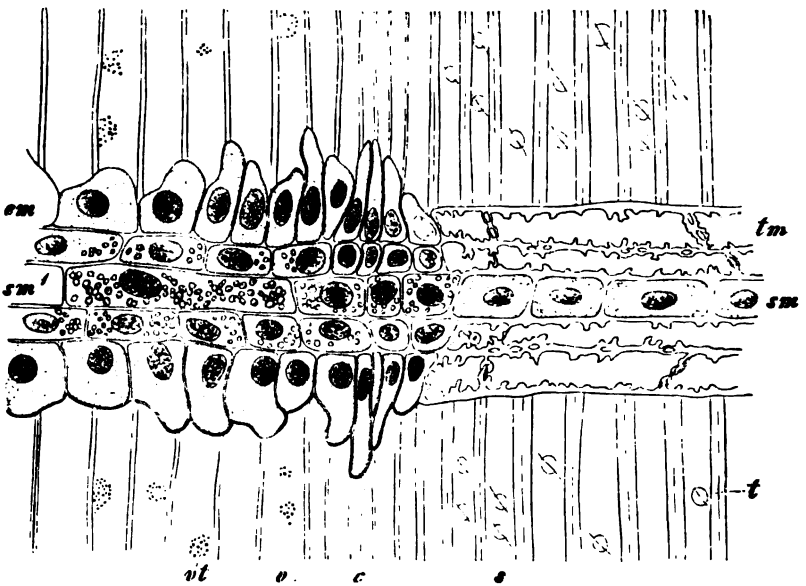


FIG. 176.—Radial section of a Pine stem, at the junction of the wood and bast. *s*, Autumn tracheides; *t*, bordered pits; *c*, cambium; *v*, sieve-tubes; *vt*, sieve-pits; *tm*, tracheidal medullary ray cells; *sm*, medullary ray cells in the wood, containing starch; *sm'*, the same, in the bast; *em*, medullary ray cells, with albuminous content. (× 240. After SCHENCK.)

place; they also conduct water from the wood outwards. The medullary rays are suited to perform these functions, since, as has been seen, they extend into both the wood and the bast (Figs. 175 *B*, 176, 179). The intercellular spaces communicate with the intercellular system of the cortex and allow of the necessary gaseous exchanges between the living cells in the wood and the external atmosphere.

In certain Gymnosperms, especially the Pines, single rows of cells of the medullary ray in the wood (usually the marginal rows) are tracheidal and without living contents; they are connected with one another and with the tracheides by means of bordered pits (Fig. 176 *tm*). They are protected against compression by the living turgescent cells of the medullary ray by means of special thickening of

their walls. These tracheidal cells facilitate the conduction of water in the radial direction between the tracheides, which are only pitted on their radial walls. In most other Conifers, in which such tracheidal elements in the medullary rays are wanting, there are tangentially-placed bordered pits in the tracheides of the wood, and these allow of the movement of water in a radial direction. The parenchymatous cells of the medullary rays of the wood are connected with the tracheides by means of large pits bordered on one side (Fig. 177 *et*).

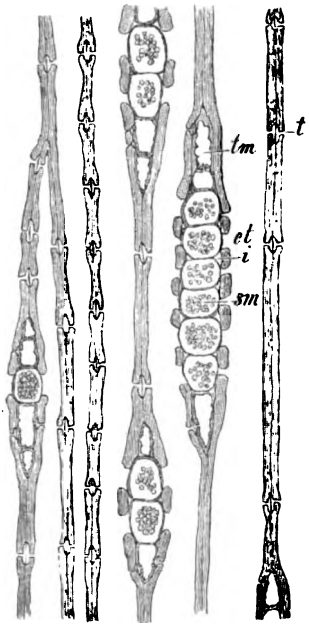


FIG. 177. — Tangential section of the autumn wood of a Pine. *t*, Bordered pit; *tm*, tracheidal medullary ray cells; *sm*, medullary ray cells containing starch; *et*, pit bordered only on one side; *i*, intercellular space in the medullary ray. (× 240. After SCHENCK.)

Owing to climatic variations, the cambial tissue of Gymnosperms, as of most Dicotyledons, exhibits a periodical activity which is expressed by the formation of ANNUAL RINGS (79) of growth (Figs. 178, 179). In spring, when new shoots are being formed, wider tracheal elements are developed than in the following seasons (Fig. 175 *A*). For this reason a difference is perceptible between the EARLY WOOD (spring wood), which is composed of large elements especially active in the conveyance of water (Fig. 175 *f*), and the LATE WOOD (autumn wood), consisting of narrow elements which impart to a stem its necessary rigidity (Figs. 175 *A*, *s*, 179). Throughout the greater part of the temperate zone, the formation of wood ceases in the latter part of August until the following spring, when the larger elements of the spring wood are again developed. Owing to the contrast in the structure of the spring and the autumn wood, the limits (Figs. 175 *g*, 179 *i*) between successive annual rings of growth become so sharply defined as to be visible even to the naked eye, and thus serve as a means of computing the age of a plant. The limits between the annual rings are less evident in the root, all the wood resembling spring wood. The cambium of the root may remain active throughout the winter and only pass into a resting condition at the commencement of the new vegetative period.

In a stem or root that has undergone secondary thickening fewer annual rings will be seen on the cross-section the nearer this is made to the growing point. The older annual rings and the older layers of bast disappear in order of their age as the tip is approached.

Under certain conditions the number of annual rings may exceed the number of years of growth. When the leaves are destroyed by frost, caterpillars, or other

injurious influences, the buds destined for the succeeding spring may unfold, and the formation of the new foliage brings about a second formation of spring wood. On the other hand, woody plants that usually have definite annual rings may exceptionally show a smaller number of rings than that corresponding to their age, owing to the limits between some of the rings not being clearly marked. In this way the number of rings on one radius of the stem may be less than when they are counted on another radius.

The wood of the stems and roots of **Dicotyledons** can be readily distinguished from that of a Gymnosperm even when only slightly magnified (Figs.

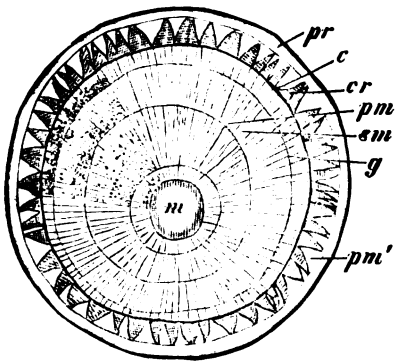


FIG. 178.—Transverse section of a stem of *Tilia ulmifolia*, in the fourth year of its growth. *pr*, Primary cortex; *c*, cambium ring; *cr*, bast; *pm*, primary medullary ray; *pm'*, expanded extremity of a primary medullary ray; *sm*, secondary medullary ray; *g*, limit of third year's wood. (×6. After SCHENCK.)

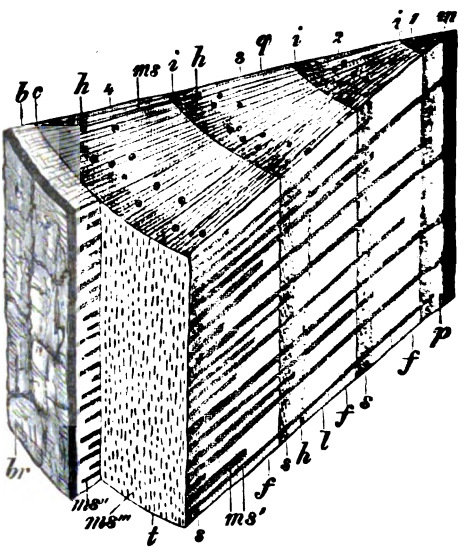


FIG. 179.—Portion of a four-year-old stem of the Pine, *Pinus sylvestris*, cut in winter. *q*, Transverse view; *l*, radial view; *t*, tangential view; *f*, spring wood; *s*, autumn wood; *m*, medulla; *p*, protoxylem; *1*, *2*, *3*, *4*, the four successive annual rings of the wood; *i*, junction of the wood of successive years; *ms'*, *ms'''*, *ms*, medullary rays in transverse, radial, and tangential view; *ms''*, radial view of medullary rays in the bast; *c*, cambium ring; *b*, bast; *h*, resin canals; *br*, bark, external to the first periderm layer, and formed from the primary cortex. (× 6. After SCHENCK.)

180, 181, 182). Not only are wood-fibres and usually wide tracheae present, in addition to tracheides and parenchyma, but the unequal growth of the various component elements leads to a departure from their original radial arrangement. In the spring wood there are numbers of very wide vessels (Figs. 180, 181 *m*), while narrow wood-fibres (*l*) and fibre tracheides (*t*) predominate in the autumn wood.

In some Dicotyledons the annual rings are not distinct because the various elements of the wood are nearly uniformly distributed in the season's growth. This is the case in the Willow, and in the Wild Vine it may be impossible to count the rings. In the woody plants of tropical regions, when there is no seasonal

interruption of growth, annual rings may also be wanting, but in many cases zones resembling the annual rings occur.

The water-conducting elements of the most recently formed annual rings are the only ones that are in direct connection with the leaves of the corresponding period of vegetation. Since there is a sudden demand for a considerable amount of water for transpiration when the leaves unfold in the spring, the provision of conducting channels in the spring wood is readily comprehensible. In many woody plants the foliage is not further increased during the summer, and the cambium can therefore form mechanical tissue in the autumn wood.

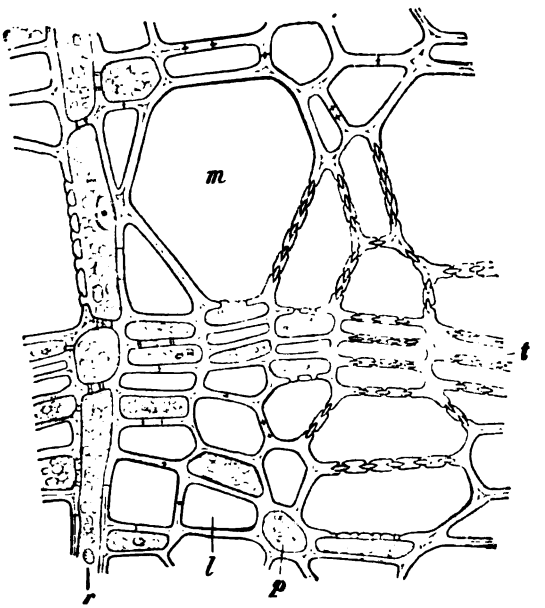


FIG. 180.—Portion of a transverse section of the wood of *Tilia ulmifolia*. *m*, Large pitted vessel; *t*, tracheides; *l*, wood-fibre; *p*, wood parenchyma; *r*, medullary ray. (× 540. After STRASBURGER.)

In spite of the variety in the structure of the wood of Dicotyledons there are some constant features in the arrangement of the different tissues. The vascular strands composed of tracheae and tracheides, while they ramify in the radial and tangential directions, form continuous longitudinal tracts from the roots to the finest tips of the branches. Were this not so the needs of the shoot-system as regards its water supply would not be met. Wood parenchyma (Figs. 180, 181 *p*), which is well developed in most dicotyledonous woods, also forms longitudinal strands or layers which, however, end blindly above and below. These form along with the medullary rays a connected system of living cells. The vessels always stand in connection with these living cells, being sometimes surrounded

by them and in other cases in contact with them on one side (Fig. 180 *p*).

The wood parenchyma surrounds the vessel in *Acacia*, etc.; it forms tangential bands in which the vessels are embedded or with which they are in contact in Walnut, Chestnut, Oak, etc.; in some cases it is limited to the outer side of the annual ring.

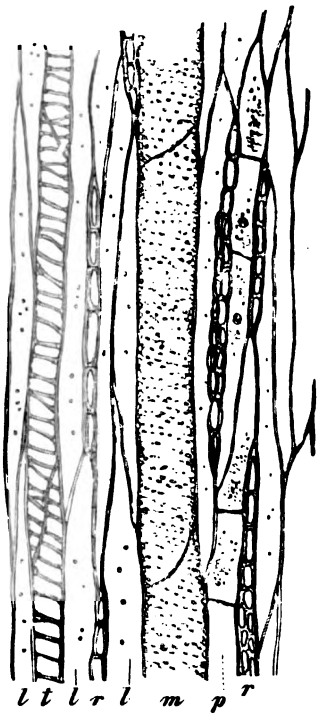


FIG. 181.—Tangential section of the wood of *Tilia ulmifolia*. *m*, Pitted vessel; *t*, spiral tracheides; *p*, wood parenchyma; *l*, wood-fibres; *r*, medullary rays. (× 160. After SCHENCK.)

The MEDULLARY RAYS (Figs. 178 *pm*, *sm*; 180, 181 *r*) resemble those of the Gymnosperms in being radially-placed bands of tissue, of greater or less vertical height, and one or a number of cells in breadth; they may be branched or unbranched (Fig. 182 *tm*, *sm*). They are continuous across the cambium into the bast (Fig. 178). The vascular strands are in contact with them at places. The parenchyma of the medullary rays thus connects the parenchyma of the bast with that of the wood, and unites all the living tissue of the stem and root into a single system. Assimilated material moving downwards in the bast can thus pass radially into the wood and be carried in this for some distance upwards or downwards, to be stored as starch in the living parenchymatous cells. The intercellular spaces, which accompany the medullary rays and the strands of wood parenchyma, allow of the gaseous exchanges necessary for the living elements of the wood.

The intervals between the strands of vessels and of parenchyma and the medullary rays are occupied by strands of wood-fibres (sclerenchyma).

The height and breadth of the medullary rays are most readily seen when they are cut across in tangential longitudinal sections of the stem; the rays then appear spindle-shaped (Fig. 181 *r*). In most woods their size varies only within narrow limits, but in others, such as the Oak and the Beech, the range is greater. In the Oak there are medullary rays which are 1 mm. wide and 1 dm. high, while numerous small rays occur between these. In the Poplar, Willow, and Box all the rays are so small as to be with difficulty distinguished even with the aid of a lens. In some lianes (*e.g. Aristolochia*) the primary rays are particularly wide and high, and may extend for the length of a whole internode.

In Dicotyledons also, as is very well shown in the Willow, the marginal cells of the medullary rays usually stand in relation to the adjacent water-conducting elements by means of pits bordered on one side; these living cells are higher than those of the middle rows (Fig. 182 *tm*). The latter are more extended radially and have no special connection with the water-conducting elements. They serve for the conduction and storage of assimilated materials (Fig. 182 *sm*).

The parenchymatous cells of the medullary rays and of the wood which adjoin the vessels take water from the latter and hand it on to the other living cells. In spring, on the other hand, they pass a large part of the stored assimilated material (especially glucose and small amounts of albuminous substances) into the vessels, so that these substances can be quickly transported to the places where

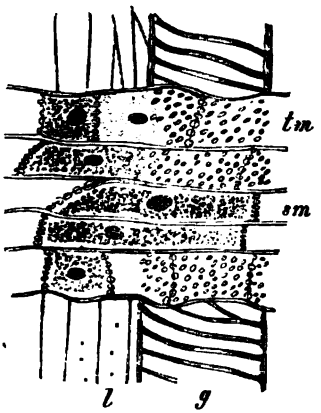


FIG. 182.—A radial section of the wood of *Tilia ulmifolia*, showing a small medullary ray. *g*, Vessel; *l*, wood fibres; *tm*, medullary ray cells in communication with the water-channels by means of pits; *sm*, conducting cells of the medullary ray. (× 240. After SCHENCK.)

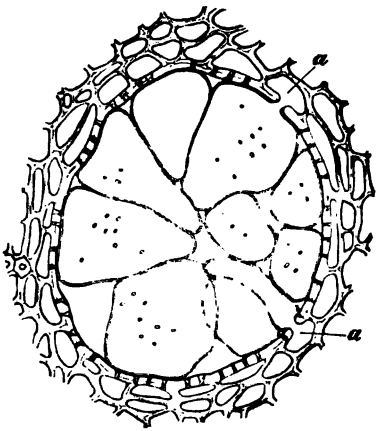


FIG. 183.—Transverse section of a vessel from the heart-wood of *Robinia Pseudacacia*, closed by thyloses; at *a*, *a* is shown the connection between the thyloses and the cells from which they have been formed. (× 300. After SCHENCK.)

they are required. Owing to this, sugar and proteids can be demonstrated in the vessels during the winter and early spring. These substances are also present in the sap that exudes when holes are bored in the stems of Birch, Maple, and other trees in the spring.

Grain of the Wood.—The technical value of certain woods is affected not only by the colour but by the graining. This depends in the first place on the arrangement of the annual rings and medullary rays, but also in many cases (*e.g.* Hazel) upon a wavy course of the elements of the wood; this may be brought about by the crowded arrangement of lateral or adventitious buds or lateral roots, or by the stimulus of wounding.

C. Subsequent Alterations of the Wood. — In the majority of trees the living elements in the more centrally-placed older portions of the woody mass die and the water channels become stopped up, leading to the formation of what is known as the

HEART-WOOD. Only the outer layer of the wood composed of the more recently-formed annual rings thus contains living cells and constitutes the SPLINT-WOOD. Reserve materials can only be stored in the splint-wood, and water-conduction is also limited to this, and indeed to its outermost portion, since, as has been seen, it is only the peripheral vessels that are in connection with the leaves and the youngest lateral roots. The heart-wood serves only for strength. Less commonly the whole of the wood persists as splint-wood (species of Maple, Birch). The heart-wood is usually darker in colour than the splint-wood and is also denser, harder, and stronger; it is protected against decay by impregnation with various substances. In other cases the heart-wood is not distinct in colour from the splint-wood and readily decays; this leads to the hollow stems so often found in old Willows.

The whitish yellow splint-wood contrasts most strongly with the heart-wood when the latter is dark in colour; thus in the Oak it is brown and in the Ebony (*Diospyros*) black. The heart-wood appears to be more durable the darker it is. Before their death the living cells of the wood, which lose their reserve materials, usually form various organic substances, especially tannins, which impregnate the walls of the surrounding elements, while resinous and gum-like products accumulate in the cavities. The tannins preserve the dead wood from decay, and their oxidation products give its dark colour. The vessels are sometimes occluded by accumulations of gum, and at other times by cells which fill up the lumen more or less completely, and are spoken of as THYLOSES (80) (Fig. 183); they originate by the adjoining living cells growing into the vessels through the pits, the membrane of which they press inwards. Thyloses also form in wounded vessels and occlude the lumen. Inorganic substances are not uncommonly deposited in the heart-wood; thus calcium carbonate occurs in the vessels of *Ulmus campestris* and *Fagus sylvatica*, while amorphous silicic acid is deposited in the vessels of Teak (*Tectona grandis*). Colouring matters are obtained from the heart-wood of some trees, *e.g.* Haematoxylin from *Haematoxylon campechianum L.* (Campeachy-wood, Logwood).

4. The Bast. A. Kinds of Tissue and their Functions.—Three types of tissue can also be distinguished in the bast (Figs. 175 *B*, 184): (1) Longitudinally-running strands of SIEVE-TUBES (*v*) with, in the Dicotyledons, COMPANION CELLS (*c*); (2) in many plants longitudinal strands of SCLERENCHYMATOUS FIBRES (BAST FIBRES) that are as a rule dead (Fig. 184 *l*); and (3) PARENCHYMA with intercellular spaces arranged both longitudinally (*p*) and in the medullary rays (Figs. 175 *B*, *m*; 184 *r*). In addition SECRETORY CELLS of various kinds may be present containing crystals (*k*) or latex. The bast, like the phloem of the vascular bundles, serves mainly to conduct the products of assimilation. It also is of use for the storage of organic substances and frequently as a mechanical tissue. In many plants the sieve-tubes have oblique end-walls (Fig. 184 *v**); they are thin-walled and unlignified, contain proteids, and usually remain functional only for a short period. The bast fibres are long and narrow and

have strongly-thickened walls that may be lignified or not. The parenchymatous cells are elongated in the direction of the strand; they are living cells with abundant reserve materials and thin unlignified walls.

At a certain distance from the cambium the sieve-plates become overlaid by callus. During the vegetative period following their development the sieve-tubes become empty and compressed together (Fig. 175 *B*, *cv*). Less often, as in the Vine, the sieve-tubes remain functional for more than one year; the callus is removed when their activity is resumed. The rows of bast parenchyma cells containing albuminous substances which are found in some Conifers undergo disorganisation at the same time as the adjacent sieve-tubes; the bast parenchyma

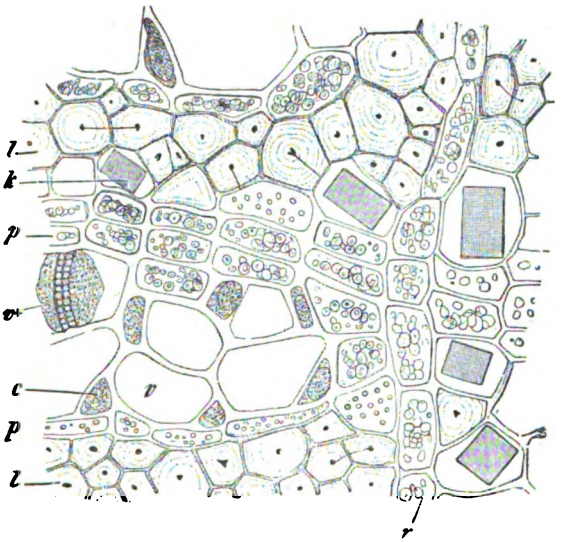


FIG. 184.—Portion of a transverse section of the bast of *Tilia ulmifolia*. *v*, Sieve-tubes; *v**, sieve-plate; *c*, companion cells; *k*, cells of bast parenchyma containing crystals; *p*, bast parenchyma; *l*, bast fibres; *r*, medullary ray. (× 540. After STRASBURGER.)

cells which contain starch, on the other hand, continue living for years, and even increase in size, while the sieve-tubes become compressed.

B. Arrangement of the Tissues in the Bast. — This resembles the arrangement in the wood. The strands of sieve-tubes form branched tracts in which the sieve-tubes have a continuous course from the roots to the foliage. The sieve-tubes, and the longitudinally-running bast parenchyma, are related at intervals to the medullary rays (Fig. 179 *ms''*), which have been seen to be the continuation of the medullary rays of the wood. Thus the products of assimilation from the foliage can either pass in the bast towards

the roots or through the medullary rays to be stored in the living cells of the wood.

The different tissues of the bast are often arranged in very regular tangential bands only interrupted by the medullary rays (Fig. 184). The periodicity of the cambium is not, however, evident in the bast, and there are no annual rings. The cambium continues to produce bast after the formation of the autumn wood has ceased.

In the Lime, for example (Fig. 184), there is an alternation of zones of sieve-tubes (*v*) with companion cells (*c*), starch-containing bast parenchyma (*p*), cells containing crystals (*k*), bast fibres (*l*), and flattened cells of bast parenchyma (*p*), followed again by sieve-tubes. The differences in the appearance of the bast of

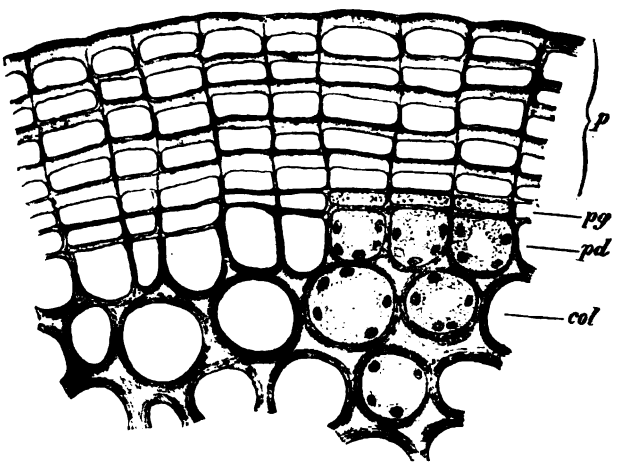


FIG. 185.—Transverse section of the outer part of a one-year-old twig of *Pyrus communis* made in autumn. It shows the commencement of the formation of the periderm. *p*, Cork; *pg*, phellogen; *pd*, phelloderm; *col*, collenchyma. The cork cells have their outer walls thickened and have brown dead contents. (× 500. After SCHENCK.)

different woody plants are due to the greater or less diameter of the sieve-tubes, the presence or absence of bast fibres, and to the mode of arrangement of the various elements.

In the Pine and various other Abietineae, rows of cells with abundant albuminous contents occur at the edges of the medullary rays (Fig. 176 *em*). They are in close contact with the sieve-tubes and connected with them by sieve-pits, and become empty and compressed at the same time as the sieve-tubes. In Dicotyledons the medullary rays in the bast are more simply constructed than in the wood. The pitting of the cells of the medullary rays of Dicotyledons, which connects them not only with the bast parenchyma but also with the companion cells of the sieve-tubes, stands in relation to the taking up of assimilated material as it is passing downwards.

Effect of the Secondary Thickening on the Tissues external to the Cambial Ring. 1. Dilatation.—Since the cambium continues

to form wood to the inside, and bast to the outside, the stem or root exhibits a secondary increase in thickness. Those permanent tissues which are situated externally to the cambial ring (the epidermis, cortex, primary phloem, and the bast) are naturally affected by this. They are tangentially stretched, compressed, displaced, or torn; they may also grow in the tangential direction (DILATATION). This latter process is naturally limited to the living cells of the cortex, the phloem, and the bast, including those of the medullary rays; in some woody plants even the epidermal cells take part in the dilatation (81). All these cells may grow considerably in the tangential direction and then become divided by radial walls. In the bast such growth is frequently very marked in the case of the medullary rays; in the Lime this leads to the formation of a secondary meristem which gives off rows of parenchymatous cells to either side in the tangential direction, so that the medullary rays of the bast widen year by year towards the outside (Fig. 178 *pm'*). The sieve-tubes and their companion cells, which only remain functional for a short time and then die, are compressed along with the secretory cells. The sclerenchymatous cells of the cortex and bast, which are usually non-living elements, also take no part in the dilatation. When a hollow cylinder of sclerenchyma is present in the cortex (Fig. 186 *sc*), it becomes torn in the tangential direction; the parenchymatous cells grow into the spaces, and in many plants become transformed into thick-walled stone cells (Fig. 186 *s*). Parenchyma cells, or groups

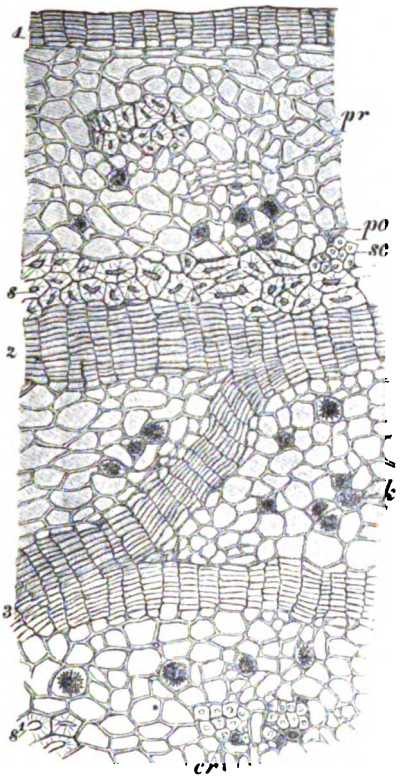


FIG. 186. — Transverse section of the peripheral tissues of the stem of *Quercus sessiliflora*. *1*, *2*, *3*, Successively formed layers of cork; *pr*, primary cortex, modified by subsequent growth; internally to *pc*, pericycle; *sc*, sclerenchymatous fibres from the ruptured ring of sclerenchymatous fibres of the pericycle; *s*, subsequently formed sclereides; *s'*, sclereides, of secondary growth; *cr*, bast fibres with accompanying crystal cells; *k*, cells with aggregate crystals. All the tissue external to the innermost layer of cork is dead and discoloured and has become transformed into bark. (× 225. After SCHENCK.)

of them in the cortex and bast, may also be developed as sclerenchymatous cells during the process of dilatation.

The epidermis may continue to expand for years in some species of Rose, Acacia, Holly and Maple, and in the Mistletoe. The outer walls of the cells are usually strongly thickened, and when ruptured on the surface become reinforced by new layers of thickening deposited within.

2. **Periderm.**—As a rule, however, the epidermis does not take part in the dilatation but is passively stretched and ultimately ruptured. A new limiting tissue is thus required to protect the underlying tissues from drying up. This arises as the CORK by the activity of a special secondary meristem, situated at the periphery of the organ (Fig. 185).

This CORK-CAMBIUM or PHELLOGEN is usually formed in the first season, soon after, or even before, the commencement of secondary growth. It may arise from the epidermis by tangential division of its cells. More usually, however, it is formed from the layer of cortex just below the epidermis, less commonly from a deeper layer of the cortex or from the pericycle. The last case is the rule for roots (Fig. 171 *B*, *k*). The meristem and all the products of its activity are known collectively as the PERIDERM. The cells cut off to the outer side become CORK-CELLS; those developed to the inner side become unsuberised cells with abundant chlorophyll, which round off and are added to the cortex. With the formation of the periderm the surface of the stem appears brown.

The cells formed on the inner side by the phellogen are termed collectively the PHELLODERM.

The cork-cambium is as a rule a typical initial cambium (cf. p. 46), at least when it forms both cork and phelloderm. An initial layer may, however, be wanting, *e.g.* in many Monocotyledons; in this case the permanent cells from which the cork cambium proceeds divide into a number of cells which become cork-cells, and the process is repeated in adjacent cells of the permanent tissue.

Periderm formation takes place at a later period in those plants in which the epidermis continues to expand for years; it is wanting only in the species of Mistletoe.

True cork is wanting in Cryptogams, even in the Pteridophytes. When protection is required its place may be taken by the impregnation of the cell walls with a very resistant brown substance or by the addition of suberised lamellae to the walls, that is the transformation of certain layers of cells into a cutis tissue (82).

As the result of the activity of the cork-cambium thick fissured incrustations of cork may arise as in the Cork Oak from which bottle cork is obtained. The stratification which this exhibits marks the annual increments. In other cases a corky layer with a smooth outer surface only a few layers of cells thick is formed (Figs. 59, 185). This may allow of the secondary growth in thickness of the stem continuing for a long time before it ultimately becomes torn and is shed.

Bottle cork (Fig. 58) is formed of thick layers of soft wide cork-cells, interrupted by thin layers of flat cork-cells marking the limits of the year's growth; this can be recognised in an ordinary cork. The pores filled with a loose powder which penetrate the whole thickness of the cork in a radial direction are the lenticels (cf. p. 59). The first layer of cork of the Cork Oak is artificially stripped off down to the cork-cambium after fifteen years. A new cambium then forms a few cells deeper which provides the cork of economic value; this is removed every 6 to 8 years. Since such dead coatings of cork cannot keep pace with the dilatation of the stem they gradually become fissured.

3. Formation of Bark.—All tissues external to the cork-cambium are cut off from supplies of water and food materials and consequently die. The dead tissue, including the layer of periderm, is termed BARK. According to the depth at which the periderm is formed this may include only the epidermis or a larger or smaller proportion of the cortex. The first layer of cork-cambium in stems and roots usually soon ceases to be active; this does not happen in the Beech. A new layer of cork forms deeper in the stem, and its activity in turn comes to an end; another layer forms still more deeply as shown in Fig. 186. Ultimately the layers of cork are forming in secondary tissues, in the living parenchyma of the zone of bast; thus in old stems all the living tissue external to the cambium is of secondary origin and the bark includes dead secondary tissues. These are emptied of their food material and contain only by-products of the metabolism. The bark cannot follow the further increase in thickness of the stem or root, but is cast off in scales or torn by longitudinal fissures. It forms an even more complete protection than the cork against both loss of water and overheating.

Since in the formation of bark the more external and oldest parts of the bast are thus shed, the zone of bast remains relatively thin. Mechanical tissues can only be permanent constituents of the stem when formed internal to the cambial ring, *i.e.* in the wood.

If the layers of the secondary periderm constitute only limited areas of the circumference of the stem the bark will be thrown off in scales, as in the SCALY BARK of the Pine, Oak, and Plane tree; if, on the contrary, the periderm layers form complete concentric rings, hollow cylinders of the cortical tissues are transformed into the so-called RINGED BARK, such as is found in the Grape-vine, Cherry, Clematis, and Honeysuckle.

When the bark peels off from the stem in layers this is not a purely mechanical result; it depends on an ABSCISS LAYER consisting of thin-walled cork-cells or phelloid cells (cf. p. 59) which are formed between the other layers of cork with thickened walls. These absciss layers are ruptured by the hygroscopic tensions set up in the bark. Bark which is not easily detached becomes cracked by the continued growth in thickness of the stem, and has then the furrowed appearance so characteristic of the majority of old tree-trunks.

The usual brown or red colour of bark, as in similarly coloured heart-wood, is occasioned by the presence of tannins, to the preservative qualities of which is due the great resistance of bark to the action of destructive agencies. The

peculiar white colour of Birch-bark is caused by the presence of granules of betulin (birch-resin) in the cells.

Healing of Wounds (82).—In the simplest cases among land plants the wounded cells die and become brown and dry, while the walls of the underlying uninjured cells become impregnated with protective substances and sometimes also form suberised lamellae. In the case of larger wounds in the Phanerogams a cork-cambium forming WOUND-CORK develops below these altered cells. Thus the leaf-scars left by the fall of the leaves (p. 119) are in the first place protected by the lignification and suberisation of the exposed cells, and later by the development of a layer of cork that becomes continuous with that covering the stem. The open ends of the vessels in the leaf-scar become occluded with wound-gum or thyloses or both ; the ends of the sieve-tubes become compressed and lignified.

When young tissue is exposed by a wound, a formation of CALLUS usually takes place. All the living cells which abut on the wound grow out and divide, becoming closely approximated. The surface of the new growth may at once become corky and thus afford the necessary protection. In most cases a cork-cambium forms in the peripheral layers of the callus and gives rise to cork. In stems of Gymnosperms and Dicotyledons, wounds which extend into the wood become surrounded and finally overcapped by an outgrowth of tissue arising from the exposed cambium. While the callus tissue is still in process of gradually growing over the wounded surface, an outer protective covering of cork is developed ; at the same time a new cambium is formed within the callus by the differentiation of an inner layer of cells, continuous with the cambium of the stem. When the margins of the over-growing callus tissue ultimately meet and close together over the wound, the edges of its cambium unite and form a complete cambial layer, continuing the cambium of the stem over the surface of the wound. The wood formed by this new cambium never coalesces with the old wood which is brown and dead. Accordingly, marks cut deep enough to penetrate the wood are merely covered over by the new wood, and may afterwards be found within the stem. In like manner, the ends of severed branches may in time become so completely overgrown as to be concealed from view. The growing points of adventitious shoots often arise in such masses of callus. As the wood produced over wounds differs in structure from normal wood, it has been distinguished as CALLUS WOOD. It consists at first of almost iso-diametrical cells, which are, however, eventually followed by more elongated cell forms. In the Cherry instead of normal wood-elements nests of thin-walled parenchymatous cells which undergo gummosis (p. 39) are produced on wounding the cambium.

Restitution.—Secondary tissues often take part in the process of restitution, *i.e.* the replacement of parts that have been lost.

In the more highly organised plants the direct replacement of lost parts is extremely rare. It occurs most readily in embryonic organs, such as growing points, when portions have been lost, and is most often found in seedlings. Thus in seedling plants of *Cyclamen* even a severed leaf-blade has been found to be replaced. As a rule, however, when regeneration processes are requisite in higher plants, and the necessary preformed organs are not present in a resting or latent condition, the older tissues return to the embryonic condition and give rise to new growing points of shoots. Since this provision for the indirect replacement of lost parts exists in plants, the fact that direct regeneration is far more frequent among animals than plants is readily comprehensible.

2. Adaptations of the Cormus to its Mode of Life and to the Environment (84)

The form and structure of the cormus are closely connected with its mode of life, which in turn depends on the environment. Practically all plants thus appear adapted to the environments in which they are usually found. The uniform physiognomy exhibited by the plants of any locality, as well as the differences in the physiognomy of the vegetation in localities which differ in climate, depend upon this. The vegetative organs are therefore not typically constructed in all cormophytes, but are frequently altered or metamorphosed in a variety of ways. Very careful developmental or anatomical investigation may be required to show that the variously-constructed organs of many cormophytes are derived by the metamorphosis of the three primary organs, root, stem, and leaf, and to ascertain with which of these any particular structure is really homologous. The external form and the functional activity of mature organs may be very misleading. One organ may assume the form and functions of another, *e.g.* a stem resembling a leaf; different primary organs may take on the same forms in relation to performing the same functions and thus be analogous but not homologous. As a rule, however, when all the characters of an altered organ are taken into consideration, some will leave no doubt as to its morphological origin.

The form of a plant and of its parts is determined in the first place by its mode of nutrition. Thus there are striking and important morphological differences between cormophytes which require only inorganic food materials (AUTOTROPHIC PLANTS) and those which require organic food (HETEROTROPHIC PLANTS).

A. Autotrophic Cormophytes

The green plants are structurally adapted to autotrophic life. The typical features of the construction of autotrophic cormophytes have been described above. The green cormophytes may exhibit considerable variety among themselves, for their structure is adapted to the different features of the environments in which they occur.

Among the numerous factors in the differing external conditions WATER and LIGHT have by far the greatest influence on the form of green plants. This is evident, for the plant can only carry on its life when sufficient water is available, and only when there is sufficient light can it construct organic substance from inorganic food materials and thus be autotrophic.

(a) Adaptations to the Humidity of the Environment

1. Water Plants. Hydrophytes (85).—Special peculiarities in structure are found in plants which live in water. These can

absorb both water and nutrient salts and also the necessary gases (carbon dioxide and oxygen) from the water by the whole surface of their stems and leaves. In considering the conditions of life in water it is essential to know the amounts of various gases which can be dissolved and to contrast this with their presence in the atmosphere. One litre of air contains about 210 c.cm. oxygen and 0·3 c.cm. of carbon dioxide. In one litre of water at 20° C., on the other hand, there can be dissolved only about 6 c.cm. oxygen, but 0·3 c.cm. carbon dioxide. There is thus available for the submerged plant as much carbon dioxide, or even somewhat more. There is, however, little oxygen, especially in the case of still water, since the diffusion of this gas in water is very slow.

Roots may be absent (*Utricularia*, *Ceratophyllum*, *Wolffia*) or only serve to attach the plant to the soil. The shoot, on the other hand, has become similar to a root, in that the thin walls of its epidermal cells have a very thin cuticle that offers little hindrance to the entrance of water. The large surface exposed by the fine subdivision of the lamina of the submerged leaves (*Batrachium*, Fig. 138, *Utricularia*, *Myriophyllum*, *Ceratophyllum*) stands in relation to the slowness of the diffusion of gases in water; floating and aerial leaves of water plants, on the other hand, are typically formed (heterophylly, cf. p. 116). As regards their anatomy the submerged leaves are characterised by the absence of stomata, and usually of hairs from the epidermis, the cells of which contain chlorophyll; the mesophyll has large intercellular spaces, and consists of uniform parenchyma, not showing the distinction of palisade and spongy tissue. The leaves in transverse section thus appear bilaterally symmetrical (Fig. 187). The feeble development of water-conducting elements in the stems and leaves, and the absence of secondary thickening, are related to the absence of transpiration, and of active transport of water. The support afforded by the surrounding water renders mechanical tissues unnecessary; the pulling forces exerted in quickly-flowing water are met by the central position of the vascular bundle.

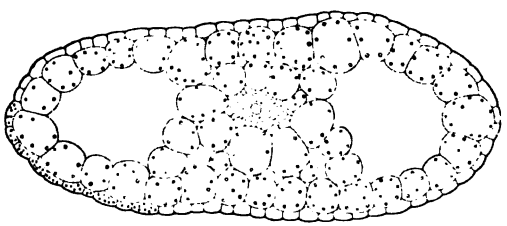


FIG. 187.—Transverse section of the leaf of *Zannichellia palustris*. (× 146. After SCHENCK.)

The great development of the intercellular spaces is a striking feature of almost all aquatic and marsh plants. They are wide, and form a regular system of air-filled chambers and passages, which are separated by parenchymatous partitions, usually only one cell thick:

this is the case, for example, in the stems of *Papyrus*, *Potamogeton*, etc., in the petioles of the Nymphaeaceae, and in the roots of *Jussieua*. Such tissue is termed AERENCHYMA. Since its wide air-passages serve for the storage of air, and allow of ready diffusion of gases within the body of the plant, the rapid transport of oxygen from the assimilating green organs to the colourless organs greatly facilitates respiration.

In some swamp plants, the subterranean organs of which are in swampy soil with little oxygen, special organs are concerned with obtaining this gas; respiratory roots (PNEUMATOPHORES, Fig. 188) grow erect from the muddy soil, obtaining oxygen from the air by lenticel-like PNEUMATHODES, and conducting it by the aerenchyma to the subterranean parts. Such plants are found among the Palms and in the Mangroves of tropical coasts, some of which are also anchored to the mud by a system of aerial stilt-roots springing from the shoots (Fig. 189) ([84]).

FIG. 188.—Respiratory roots of *Sonneratia alba*. (Reduced from a figure in *Vegetationsbildern* by JOH. SCHMIDT.)

2. Land Plants.—These usually obtain water and nutrient salts from the soil, and oxygen and carbon dioxide from the atmosphere; their aerial shoots give off water in the form of vapour in the process of transpiration.

A few plants of very moist habitats, especially the Hymenophyllaceae of tropical forests, which can absorb water by the general surface, form an exception. Some of them develop no roots but have a system of water-absorbing hairs on their stems or leaves which considerably increase the absorbent surface.

The construction of land plants differs according to their occurrence in constantly moist localities, dry localities or climates, or intermittently moist climates.

(a) Adaptations to constantly moist Habitats. Hygrophytes ([86]). —Terrestrial plants which inhabit situations in which the atmosphere is permanently moist, such as many tropical shade plants, are spoken of as HYGROPHILOUS or HYGROPHYTES. Like water plants they have no need of arrangements to diminish transpiration but, on the

contrary, require to facilitate the giving off of water from the aerial shoots. Only in this way can a sufficiently active movement of water from the roots in the soil to the organs above ground be ensured to supply the requisite quantity of nutrient salts. Many hygrophytes, especially those that inhabit the moistest situations, resemble water plants in form and structure.

FIG. 189.—Stilt-roots in *Rhizophora mucronata* in the Malay Archipelago. (After KARSTEN.)

Hygrophytes show a variety of arrangements to favour transpiration such as expanded thin leaf-blades, thin cuticle, and the situation of the stomata on exposed projections raised above the general surface. There are also peculiarities in their leaves which, as STAHL showed, tend to get rid of the water after heavy rainfall as quickly as possible. Thus a drawn-out tip to the leaf-blade (DRIP-TIP) or waxy coatings rendering the surface of the leaf unwettable facilitates the shedding of water from the leaf; while a velvety surface, due to the presence of papillae, spreads drops of water by capillary action into an extremely thin film which readily evaporates. According to STAHL also the presence of pigments which absorb the rays of light and heat falling on variegated leaves raise the temperature of the leaf and maintain transpiration even in a saturated atmosphere. In guttation or the giving off of drops of liquid water from water-excreting organs or HYDATHODES, some of these plants have the means of giving off sufficient water when transpiration is completely stopped. These organs are glandular surfaces or hairs which secrete water, or are special clefts in the epidermis through which water derived from the vascular bundles is forced (cf. Fig. 131).

(b) Adaptations to physiologically dry Habitats or to dry Climates. Xerophytes ([84, 87]). Plants, the shoots of which are exposed to dry air while they have difficulty in obtaining an adequate or sufficiently rapid supply of water to make good the loss in transpiration, require arrangements to diminish the latter process. The ordinary limitation of transpiration by closure of the stomata is not sufficient in the case of plants of exceptionally dry habitats or climates. Only a few cormophytes can withstand drying up, as do many Lichens and Bryophyta (cf. p. 222), and most of them die when wilting is carried far.

Plants with such arrangements to diminish the loss of water are termed XEROPHILOUS or XEROPHYTES. They are recognisable by their general habit. The morphological peculiarities which are

involved in arrangements to diminish transpiration are referred to collectively as the xerophytic structure (XEROMORPHY). Desert plants, the plants of dry rocks and many epiphytes, are naturally extreme xerophytes (cf. p. 183).

It is, however, a striking fact that xerophytic structure is also met with in plants of quite different modes of life, where it is not at first sight comprehensible, *e.g.* in plants of high mountains or of high latitudes, in many swamp plants, in plants of the sea-coast (HALOPHYTES) (Fig. 195), even when, as in the case of the Mangrove vegetation of tropical coasts, they grow directly in the water, and lastly in many trees of the tropical rain-forest. Though much is still obscure regarding this, it is safe to assume that the majority of these plants are, at least periodically, in danger of losing more water by transpiration than they can make good by absorption from the soil. When they occur in relatively moist soils these appear to be more or less physiologically dry for the plants, *i.e.*, to be such as to render the absorption of water difficult.

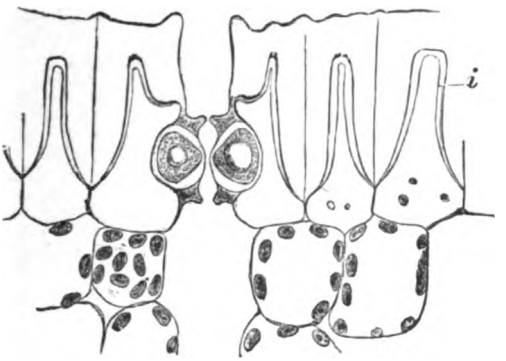


FIG. 190.—Transverse section of the epidermis of *Aloe nigricans*. *i*, Inner, uncutinised thickening layer. (× 240. After STRASSBURGER.)

Both morphological and anatomical arrangements are concerned in diminishing transpiration. Some of these adaptations may at the same time be protective against strong insolation or overheating.

The following are **anatomical** features which serve to diminish transpiration: thick epidermal cell walls and cuticle; formation of waxy and resinous coatings, and, in the case of stems and roots, layers of cork; reduction in the number of stomata; narrowing of the stomata and their occlusion by resin; sinking of the stomata below the general level of the epidermis, either singly (Fig. 190) or in numbers in special flask-shaped depressions of the under side of the leaf (*e.g.* Oleander), or the over-arching of the stomata by adjoining cells so that they come to be situated in cavities protected from the wind. Hairs, whether woolly, stellate, or scaly, which early become filled with air and give the plants a whitish or grey appearance (Edelweiss, Australian Proteaceae, Olive), may serve as a protection against the sun's rays. On the other hand, evergreen leaves may be small, leathery, and relatively poor in sap (*e.g.* sclerophyllous evergreen

plants of the Mediterranean region, such as the Laurel and Myrtle). The small size of the intercellular spaces in the mesophyll is characteristic of the leaves of well-marked sclerophylls (Fig. 193); there is often no spongy tissue, but frequently several layers of palisade cells beneath both upper and lower epidermis so that the structure of the leaf becomes bilaterally symmetrical. Some xerophytes are independent of such protections against transpiration, since their highly concentrated cell sap enables them to absorb water from very dry soil (p. 228).

These anatomical arrangements are usually associated with **morphological** peculiarities of the **external form.**

Many xerophytes with small leaves have the branches crowded together to form a dense cushion (*e.g.* many Alpine plants, Fig. 191); not only is transpiration checked by this, but a protection against too strong insolation is obtained.

FIG. 191.—*Raoulia mammillaria* from New Zealand, showing the cushion-like shape of the individual plant. (From SCHIMPER'S *Plant-Geography.*)

A very effective protection against transpiration and light is obtained by the leaf surface being placed vertically (Australian Acacias and Myrtaceae); this is often associated with a reduction of the lamina and a flattening of the petiole (PHYLLODES, Figs. 136, 192). A similar position of the leaves is met with in some of our native plants such as *Lactuca scariola*, the Compass Plant in which all the leaves stand vertically and in the direction of north and south. Such leaves avoid more or less completely the rays of the sun when this is at its highest, and excessive heating and transpiration are thus prevented.

Very commonly the leaf surface is reduced.. This takes place in the grasses of exposed situations by the inrolling of the upper surface (Fig. 194). In the Ericaceae, Genisteae, Cupressaceae, and some New Zealand species of *Veronica* (cf. also Fig. 195), it is effected by reduction of the lamina, which is completely lost in Cactaceae, in tree-like species of *Euphorbia*, and in some Asclepiadaceae. With the reduction in the leaf-surface the assimilation of carbon is also diminished, and a compensatory development of chlorophyll-containing parenchyma takes place in the stems of such plants. The twigs of the Broom (*Sarothamnus scoparius*), which bear only occasional leaves that are soon shed, are elongated and green (sclerocaulous plants).

A striking modification is exhibited by shoots which only develop reduced leaves, while the stems become flat and leaf-like and assume the functions of leaves. Such leaf-like shoots are called CLADODES or PHYLLOCLADES, and GOEBEL proposes to distinguish those flattened shoots which have limited growth and specially leaf-like appearance as phylloclades, and to term other flattened axes cladodes. An instructive example of such formations is furnished by *Ruscus aculeatus* (Fig. 196), a small shrub of the Mediterranean region whose stems bear in the axils of their scale-like leaves (*f*) broad sharp-pointed cladodes (*cl*) which have altogether the appearance of leaves. The flowers arise from the upper surface of these cladodes, in the axils of scale leaves. These phylloclades afford a good example of the analogy between organs. Their appearance and functions are those

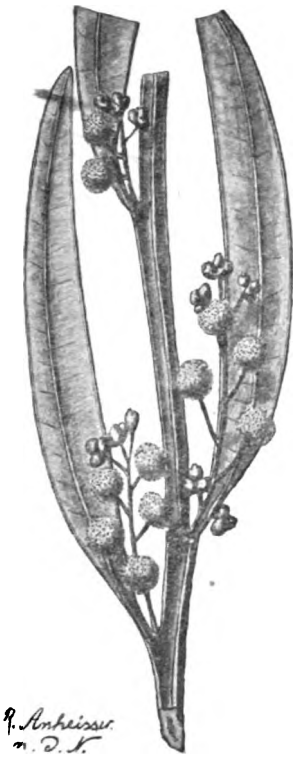


FIG. 192.—*Acacia marginata*, with vertically-placed phyllodes. (From SCHIMPER's *Plant-Geography*.)

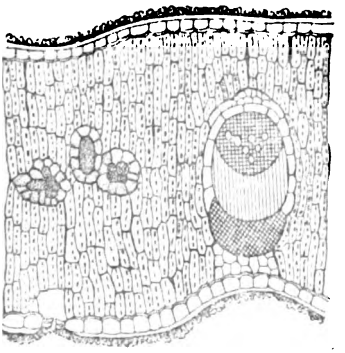


FIG. 193.—Transverse section of the leaf of *Capparis spinosa*, var. *aegyptiaca*. (× 40. SCHIMPER after VOLKENS.)

of leaves, but the morphological features mentioned above show that they are shoots. A leaf-like flattening of the massive stems which thus form cladodes is met with in the well-known Opuntias (Fig. 197), the bases of the branches remaining narrow.

The great development of sclerenchyma in the shoots of many xerophytes is associated with the development of THORNS. Thus spiny shoots, though not lacking in other regions, are characteristic of many xerophytes of deserts and steppes. The thorns are lignified

and rigid pointed structures that may either be unbranched or branched. They originate by the modification of leaves or parts of leaves (LEAF-THORNS), of shoots (SHOOT-THORNS), or less commonly of roots (ROOT-THORNS). In the Barberry (*Berberis vulgaris*) the leaves borne on the main shoots are transformed into thorns which are usually tri-radiate, while the lateral branches bearing the foliage leaves stand in the axils of these thorns. In the Cactaceae also (Fig. 197) the thorns arise from leaf-primordia. In *Robinia* (Fig. 198), and in the succulent species of *Euphorbia*, the two stipules of each leaf

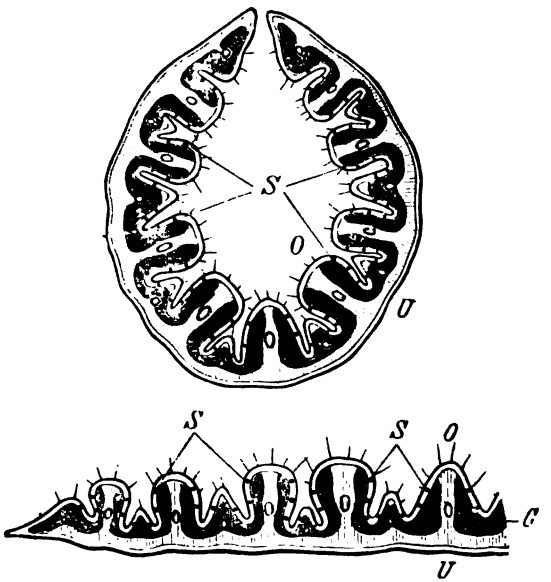


FIG. 194.—Transverse sections of the leaf of *Stipa capillata*. The leaf above in the closed state, the half leaf below expanded. *U*, lower surface, without stomata; *O*, upper surface, with stomata (*S*); *C*, chlorophyllous mesophyll. (× 30. After KERNER VON MARILAUN.)

form thorns. Shoot-thorns are found in *Prunus spinosa*, *Crataegus oxycantha*, and *Gleditschia* (Fig. 199). In *Colletia cruciata* all the shoots are flattened and spiny, so that, in addition to serving as protective structures, they perform the duties of the leaves which are soon lost. The plant is an American shrub belonging to the Rhamnaceae and grows in dry sunny situations. Root-thorns occur on the stems of some Palms (*e.g. Acanthorrhiza*).

Xerophytes may have swollen or succulent leaves or stems. The green, columnar, prismatic, cylindrical, or globular Euphorbiaceae and Cactaceae are examples. Many xerophytes not merely utilise water economically, but, when it is obtainable, store water in special tissues against periods of need. When typically developed such water-storage

tissue consists of large colourless cells containing a large vacuole. Every epidermal cell may be regarded as storing water. In some cases, however, the epidermal cells attain a huge size and constitute a large proportion of the leaf, or they may be divided parallel to the upper surface and give rise to a many-layered water tissue (various

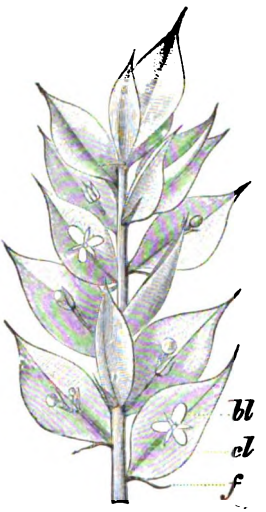


FIG. 196.—Twig of *Ruscus aculeatus*. *f*, Leaf; *cl*, cladode; *bl*, flower. (Nat. size. After SCHENCK.)

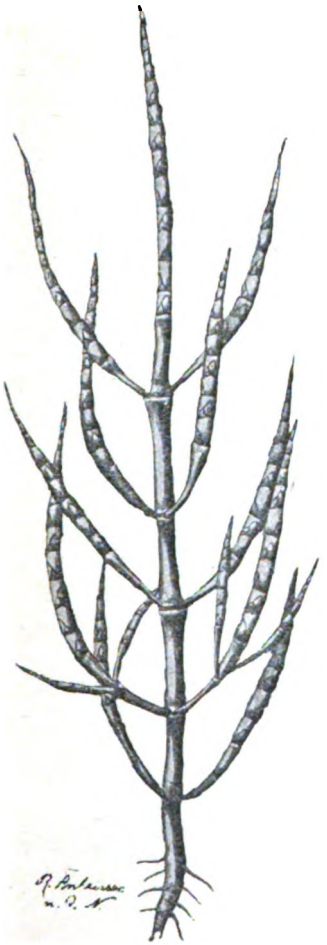


FIG. 195.—*Salicornia herbacea*, a characteristic halophyte. (From SCHIMPER'S *Plant-Geography*.)

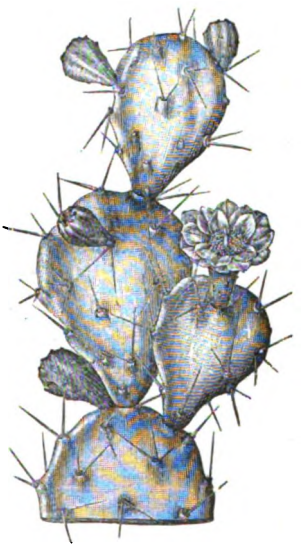


FIG. 197.—*Opuntia monacantha*, Haw., showing flower and fruit. (⅛ nat. size. After SCHUMANN.)

Piperaceae, Begoniaceae, species of *Ficus*, *Tradescantia*). The water-storage tissue often has a more central position, and when largely developed gives the character of succulent plants. In rare cases the roots are transformed for water-storage (*e.g. Oxalis tetraphylla*). Leaf-succulents are more common (*e.g. Sedum*, *Sempervivum*, *Agave*, *Aloe*, *Mesembryanthemum*), while examples of stem-succulents are afforded by the Cactaceae, species of *Euphorbia*, *Stapelia*, and other Asclepiadaceae (Figs. 197, 200) and *Kleinia* among the Compositae. The columnar or spherical Cactaceae are especially characteristic of arid regions in the new world, while Euphorbias of similar habit take their place in the eastern hemisphere. Similarity in the mode of life has thus

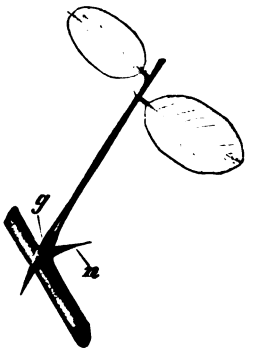


FIG. 198.—Part of stem and compound leaf of *Robinia Pseudacacia*. *n*, Stipules modified into thorns; *g*, pulvinus. (½ nat. size. After SCHENCK.)

FIG. 199.—Stem-thorn of *Gleditschia triacanthos*. (½ nat. size. After SCHENCK.)

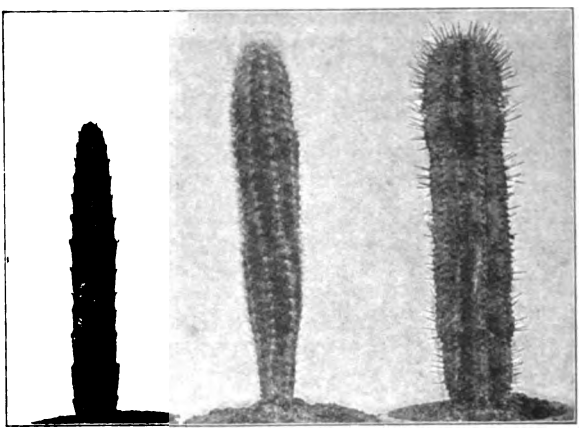


FIG. 200.—Plants with succulent stems. *a*, *Stapelia grandiflora*; *b*, *Cereus Pringlei*; *c*, *Euphorbia erosa*. (⅛ nat. size.)

brought about a corresponding form in widely distinct plants (cf. Fig. 200, *a-c*). This phenomenon of CONVERGENCE OF CHARACTERS is not infrequent. In extreme cases the form of the stem or the leaf of succulent plants may approach that of a sphere; this, for a given

volume, exposes the minimum surface and is thus advantageous in diminishing transpiration. NOLL has estimated that the loss of water from a spherical Cactus is 600 times less than from an equally heavy plant of *Aristolochia sipho.*

Special interest attaches to some xerophytes in which the stems as well as the leaves are reduced. Thus in the epiphytic orchid *Taeniophyllum* (Fig. 201) the flattened green roots represent the vegetative organs and carry on the functions of the leaves.

(c) Adaptations to periodically moist Climates. Tropophytes ([84]). In some moist and warm regions of the tropics the climate remains almost equally favourable to the growth of plants throughout the year. Wherever, however, there is a marked periodicity in the climate, with an alternation between a period favourable to the growth of plants and a more or less injurious season, a corresponding

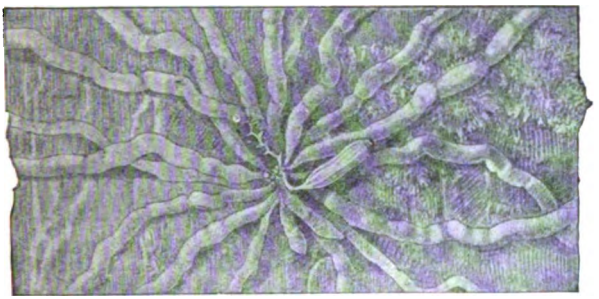


FIG. 201.—*Taeniophyllum Zollingeri.* A xerophytic orchid without leaf or stem but with green flattened roots. (Nat. size. From SCHIMPER'S *Plant-Geography*, after WIESNER.)

PERIODICITY is found in the vital processes of the plants. The resting period may be brought about either by dryness or by the cold of a winter season. Many of the plants living under such a climate show differences in structure as compared with those of uniformly moist tropical regions. Only those forms will succeed that can endure the unfavourable period in one way or another. The main danger when a cold winter alternates with a summer period lies in death from lack of water during the physiologically dry cold period. This danger does not threaten extreme xerophytes since they are suited to dry habitats in the favourable period, but does affect plants the structure of which is not xerophytic. Since the leaves as the organs of transpiration are especially concerned, the shedding of the leaves before the unfavourable period in the case of deciduous trees or the dying down of the leafy shoots in many herbaceous plants is readily understood. Further, the embryonic tissue, from which the lost parts will be replaced at the commencement of the favourable season, may require to be specially protected from the risk of desiccation.

The majority of our native cormophytic plants show such protective arrangements against an unfavourable season. In the favourable period they resemble hygrophytes in not requiring any special protection against excessive transpiration, but they behave as extreme xerophytes during the unfavourable period. Such plants are spoken of as tropophytes.

The plants of periodically moist climates may be perennial woody plants (trees and shrubs), perennial herbaceous plants, and annual herbs. Each of these groups exhibits special means of protecting the transpiring surface and the embryonic tissues against drying.

FIG. 202.—Winter buds of the Beech (*Fagus silvatica*). *kns*, Bud-scales. (Nat. size. After SCHENCK.)

1. The **woody plants** (with the exception of a few evergreens with xerophytic leaves, such as *Ilex*, and the Coniferae) shed their leaves. The evergreen and the deciduous forms alike contrast with many tropical plants in protecting the growing points within WINTER BUDS (Fig. 202).

Such buds are protected by the BUD-SCALES which are in close contact. These may be derived from entire primordial leaves that remain unsegmented but more commonly are formed from the enlarged and modified leaf-base. The upper portion of the leaf may scarcely develop or may be recognisable at the tip of the bud-scale in a more or less reduced condition. Thus in an opening bud of the Horse Chestnut (*Aesculus hippocastanum*) in the spring the small leaf-blade can be clearly seen in the case of the inner bud-scales, while it is scarcely visible on the outer scales. In other cases (*e.g.* in the Oak) the bud-scales arise from stipules and thus also belong to the leaf-base. The base of a subtending leaf may remain and cover the axillary bud after the rest of the leaf is shed.

Bud-scales are thick, leathery, and hard, and usually brown in colour. They are rendered even more effective in protecting the buds from desiccation by corky or hairy coverings, by excretions of resin, gum, or mucilage, and by the enclosure of air between the scales. Resin, etc., are usually secreted by peculiar, stalked, glandular hairs or COLLETERS (cf. Fig. 56); in the case of the winter buds of many trees (*e.g.* the Horse Chestnut) a mixture of gum and resin is thus secreted and, becoming free on the bursting of the cuticle, flows between the scales, sticking them together. When the buds open in the spring the bud-scales as a rule are shed. The internodes between them being very short, the scales leave closely crowded scars on the shoots by the help of which the growth of successive years can be recognised.

2. **The perennial herbs** sacrifice not only the leaves but whole leafy shoots with their buds, so far as these project in the air and are

exposed to the danger of drying. The buds that persist through the winter may be just above the surface of the soil but protected by fallen leaves or by snow, or they are subterranean and more effectively protected both against desiccation and frost by the surrounding earth.

When the persisting buds are above ground they may be borne on creeping surface shoots (*e.g. Saxifraga, Stellaria holostea, Thymus*, etc.), or are subterranean shoots or rhizomes, as in the perennial rosette plants (*Bellis, Taraxacum, Primula*), and in biennials which pass the winter with a rosette of leaves (*e.g. Verbascum, Digitalis*, etc.). Here also, as in the case of geophytes, subterranean storage organs may occur.

In the GEOPHYTES (88) or herbs with subterranean buds which persist through the winter, the parts which bear the buds have a construction corresponding to their life in the soil. They may be metamorphosed shoots (RHIZOMES, TUBERS, BULBS), or metamorphosed roots (ROOT-TUBERS). The buds that form new shoots in the spring require a supply of food materials, especially when they are placed some distance below the surface. These food materials were constructed in the preceding favourable season before the aerial shoots died down. The subterranean organs, formed largely of storage parenchyma, are naturally thick or swollen, to allow of the accumulation of reserve materials. Such storage organs may be modified stems, leaves, or roots. They become gradually depleted at the commencement of the period favourable for vegetation, and then (except in the case of many rhizomes) perish and are replaced.

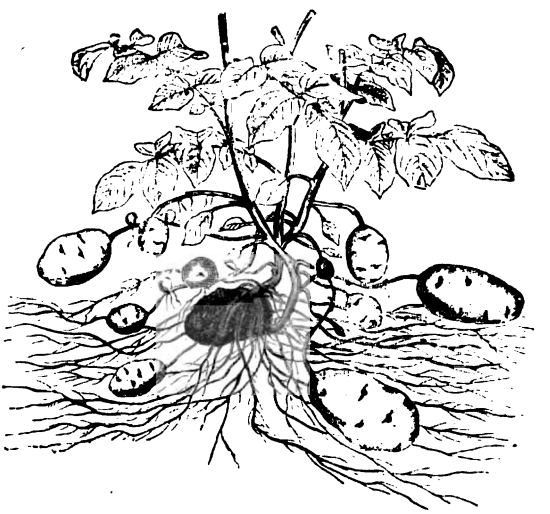


FIG. 203.—Part of a growing Potato plant, *Solanum tuberosum*. The whole plant has been developed from the dark-coloured tuber in the centre. (From nature, copied from one of BAILLON'S illustrations, ½ nat. size. After SCHENCK.)

(*a*) Root-stocks or RHIZOMES and STEM-TUBERS are colourless subterranean shoots, the former being thick or relatively thin with shorter or longer internodes (Figs. 123, 138), while the latter (*e.g.* the Potato-tuber, Fig. 203) are greatly thickened. The leaves, as is the rule in subterranean shoots, are developed as scales. The reserve materials are stored in the stem, which is on this account usually

swollen. By the presence of scale leaves, with their axillary buds, the absence of a root-cap and the internal structure, a rhizome or tuber can be distinguished from a root. While all transitions between rhizomes and shoot-tubers exist, roots are usually absent from the latter, while the rhizomes, which may grow horizontally, obliquely, or vertically, and be branched or unbranched, as a rule bear roots.

In Fig. 138 is shown the root-stock of Solomon's Seal (*Polygonatum multiflorum*), which has been already referred to as an example of a sympodium. At *c*, *d*, and *e* are seen the scars of the aerial shoots of the three preceding years; at *b* may be seen the base of the stem growing at the time the rhizome was taken from the ground, while at *a* is shown the bud of the next year's aerial growth.

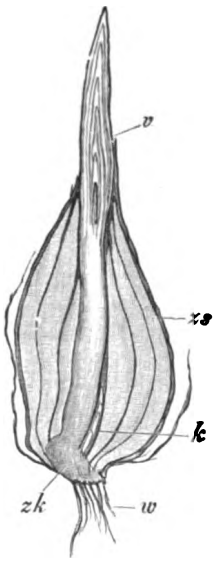


FIG. 204. — Longitudinal section of Tulip bulb, *Tulipa Gesneriana*. *zk*, Modified stem; *zs*, scale leaves; *v*, terminal bud; *k*, rudiment of a young bulb; *w*, roots. (Nat. size. After SCHENCK.)

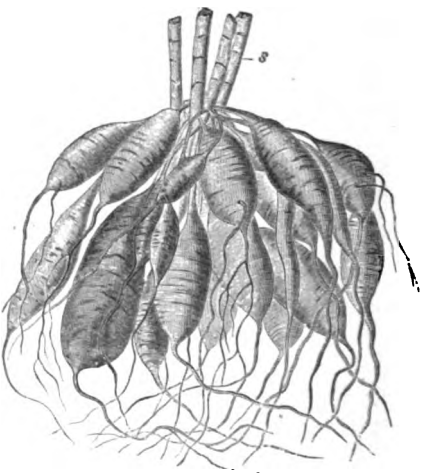


FIG. 205.—Root-tubers of *Dahlia variabilis*. *s*, The lower portions of the cut stems. (⅓ nat. size. After SCHENCK.)

The tubers of the Potato, of *Colchicum autumnale*, and *Crocus sativus*, are examples of stem-tubers. The tubers of the Potato (Fig. 203) or of the Jerusalem Artichoke (*Helianthus tuberosus*) are subterranean shoots with swollen axes and reduced leaves. They are formed from the ends of branched underground shoots or runners (STOLONS), and thus develop at a little distance from the parent plant. The so-called eyes on the outside of a potato, from which the next year's growth arises, are in reality axillary buds, but the scales which represent their subtending leaves can only be distinguished on very young tubers. The parent plant dies after the formation of the tubers, and the reserve food stored in the tubers nourishes the shoots which afterwards develop from the eyes.

In the Meadow Saffron new tubers arise from axillary buds near the base of the modified shoot, but in the Crocus from buds near the apex. In consequence of this,

in the one case the new tubers appear to grow out of the side, and in the other to spring from the top of the old tubers.

The Radish is also a tuberous stem, although only a portion of a single internode, the hypocotyl of the seedling, is involved in the swelling.

(*b*) BULBS also belong to the class of subterranean metamorphosed shoots. They represent a shortened shoot with a flattened discoid stem (Fig. 204 *zk*), the fleshy thickened scale leaves (*zs*) of which are filled with reserve food material. The aerial shoot of a bulb develops from its axis, while new bulbs are formed from buds (*k*) in the axils of the scale leaves.

(*c*) Other herbaceous perennials of periodically moist climates (*e.g.* the Dahlia and many Orchids) form ROOT-TUBERS (Figs. 205, 206). They resemble the stem-tubers, though their true nature can be recognised by the presence of a root-cap, the absence of leaves, and the internal structure. Tuberous main roots are found in the Carrot and the Beet, both of which are biennial plants.

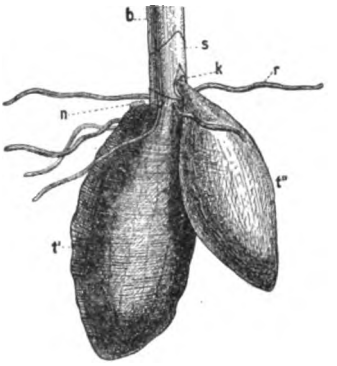


FIG. 206.—Root-tuber of *Orchis* somewhat diagrammatically represented. *t'*, The old root-tuber; *t''*, the young root-tuber; *b*, floral shoot; *s*, scale leaf with axillary bud, *k*, from which the new tuber has arisen; *r*, ordinary adventitious roots; *n*, the scar on the old tuber marking its attachment to its parent shoot. (⅓ nat. size.)

The morphology of the tubers of the Orchidaceae is peculiar. They are, to a great extent, made up of a fleshy swollen root terminating above in a shoot-bud. At their lower extremity the tubers are either simple or palmately segmented. In the adjoining figure (Fig. 206) both an old (*t'*) and a young tuber (*t''*) are represented still united together. The older tuber has produced its flowering shoot (*b*), and has begun to shrivel; a bud, formed at the base of the shoot, in the axil of a scale leaf (*s*), has already developed an adventitious root which has given rise to the younger tuber. Roots of ordinary form arise from the base of the stem above the tuber.

Many bulbs, tubers, and rhizomes occur at a SPECIFIC DEPTH, which may, however, vary with the nature of the soil. Thus the rhizome of *Paris* is placed at a depth of 2-5 cm., that of *Arum* at 6-12 cm., of *Colchicum* at 10-16 cm., and of *Asparagus officinalis* at 20-40 cm. The seeds of these plants germinate close to the surface of the soil so that the subterranean shoots of the young plants must penetrate more and more deeply into the earth. This may be effected by the movements of growth of the stem (cf. p. 345) or by contractile roots. Thus in *Lilium* (Fig. 207) all the roots are highly contractile; this is best seen in Fig. 207, 3, where the two lowest roots have con-

tracted strongly and so altered the position of the bulb that the higher roots appear curved near their attachment. When the bulb has reached the proper depth it is only drawn down each year to compensate for the onward growth of the growing point. In other cases all the roots are not contractile (*Arum*), or only one or a few contractile roots are developed (*Crocus, Gladiolus, Oxalis elegans*). While the above

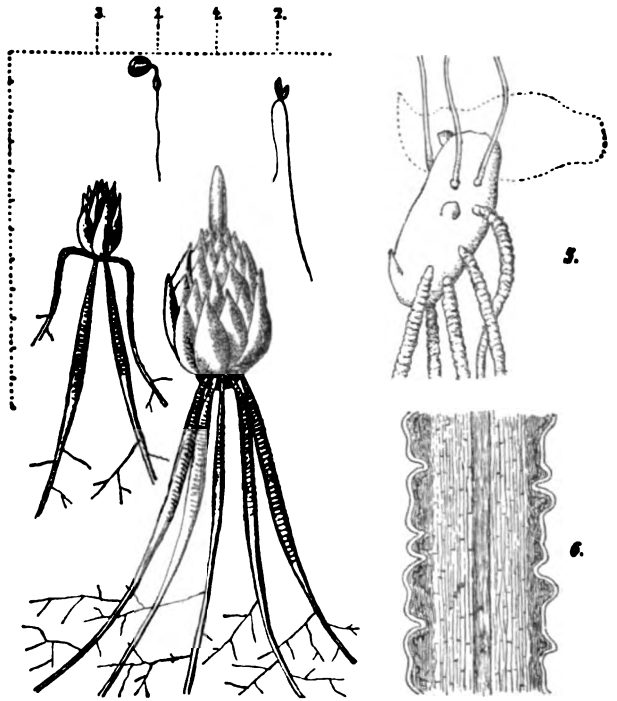


FIG. 207.—*1-4*, Germination of *Lilium martagon* (reduced). The horizontal line marks the surface of the soil; the vertical line is graduated in centimetres. *1*, Seedling attached to seed; *2*, plant at end of the second year; *3*, young plant still descending in the soil; *4*, full-grown plant at its normal depth. *5*, *Colchicum autumnale* (somewhat reduced). The original position of the tuber, which has been altered by the contraction of the roots, is shown by the dotted outline. *6*, Contracted root of *Lilium*. (× 6. After RIMBACH.)

examples are of lateral roots a similar result may be brought about by the main root. Thus in some rosette plants the main root continues to contract as secondary growth proceeds, so that the growing point of the shoot is drawn down each year as much as it is raised by its own growth, and the rosette of leaves remains pressed against the surface of the soil (*e.g. Gentiana lutea*).

3. **Annual herbs** do not retain their vegetative organs during the unfavourable season, which they pass safely in the form of dry seeds.

The more uniformly favourable for vegetation the climate is throughout the year (as in the moist tropical regions) the more do evergreen woody plants preponderate, though evergreen perennial herbs often with subterranean shoots are also present. On the other hand, as the periodicity in the climate becomes more extreme, as in the steppes with a long dry period or in climates with severe winters, the percentage of tropophytes with marked protective arrangements increases, while annual plants and geophytes preponderate among the herbs.

(b) Adaptations for obtaining Light (84)

In the luxuriant vegetation produced under favourable climatic conditions plants of large or gigantic size are met with. As mentioned

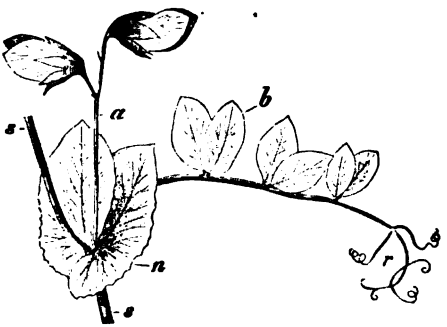


FIG. 208.—Portion of stem and leaf of the common Pea, *Pisum sativum*. *s*, Stem; *n*, stipules; *b*, leaflets of the compound leaf; *r*, leaflets modified as tendrils; *a*, floral shoot. (½ nat. size. After SCHENCK.)

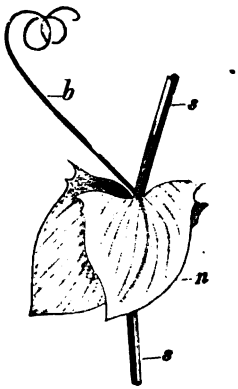


FIG. 209.—*Lathyrus Aphaca*. *s*, Stem; *n*, stipules; *b*, leaf tendril. (½ nat. size. After SCHENCK.)

above, the primeval tropical forest is composed of such large trees, beneath the shade of which larger and smaller evergreen shrubs and evergreen herbaceous plants live. The direct sunlight is in large part intercepted by the foliage of the upper strata of this vegetation.

The cuticle of the leaves of tropical trees is often smooth and reflects a portion of the light, giving rise to the characteristic glitter on the foliage in these regions. This is possibly a protective arrangement against too great insolation. Other adaptations to the same end were considered on p. 169.

The smaller SHADE PLANTS of the primeval forests and also of our native woods have usually large leaves, and are adapted to the assimilation of carbon dioxide in light of low intensity.

In the struggle for light two groups of cormophytes of characteristic construction have emerged, in addition to trees and shrubs.

These are the CLIMBING PLANTS or LIANES and the EPIPHYTES. They are specially characteristic of the tropics, though also represented in our native flora.

1. Lianes or Climbing Plants ([89]).—These are able without great expenditure of material in the construction of columnar stems to raise their foliage above the shade of the forest and obtain stronger light. Their slender stems climb by the help of the shoots, trunks, and branches of other plants. It is the rope-like stems of lianes that render many parts of the tropical jungle almost impenetrable.

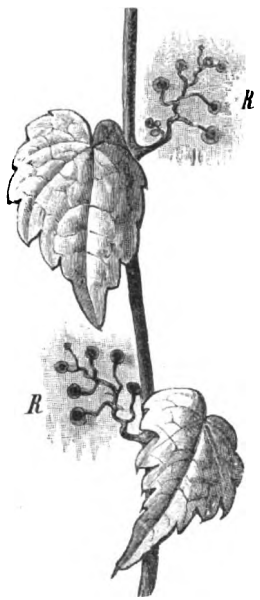


FIG. 210.—*Parthenocissus tricuspidata*. *R*, *R*, Stem-tendrils. (⅔ nat. size. After NOLL.)

Climbing is effected in a number of different ways. Some plants SCRAMBLE by means of hooked lateral shoots, by hairs and prickles, by a combination of these or by means of thorns (*e.g. Galium aparine*, Roses, *Solanum dulcamara*); others climb by means of roots (ROOT-CLIMBERS, *e.g.* Ivy, many Araceae), or by twining stems (TWINING PLANTS, *e.g.* Hop, Scarlet Runner Bean); in others tendrils are developed as special organs of attachment (TENDRIL CLIMBERS). Tendrils are slender, cylindrical, branched or unbranched organs; they are irritable to contact (cf. p. 353), and thus able to encircle supports to which they attach the plant. They may be METAMORPHOSED SHOOTS (stem-tendrils) as in the Vine, the Wild Vine (Fig. 210), and the Passion-flower. In other cases they are TRANSFORMED LEAVES as in the Gourd, the Cucumber, and *Lathyrus aphaca* (Fig. 209); in the last example the functions of the leaf-blade, which has become the tendril, have been assumed by the expanded stipules. In the Pea (Fig. 208) and many other cases the uppermost leaflets of the pinnate leaf form a branched tendril.

In some forms of the Wild Vine (*Parthenocissus quinquefolia*) and in other species of this genus such as *P. tricuspidata* (Fig. 210) the branched tendrils bear attaching discs at their tips and can thus fasten the plant to flat surfaces.

[89] The great width of the vessels and sieve-tubes is characteristic of almost all lianes. In tropical climbers anomalous secondary growth is frequently met with, resulting in a subdivided woody mass that renders the long rope-like stems capable of withstanding bending and twisting. A very peculiar structure is exhibited by many lianes of the Bignoniaceae, the wood of which is cleft by radially-projecting masses of bast (Fig. 212). The primary stem of the Bignoniaceae shows the ordinary circular arrangement of the vascular bundles. Wood and bast are at first

produced from the cambium ring in the usual manner, and an inner, normal wood cylinder of AXIAL wood is formed. Such normally-formed axial wood cylinders are common to many otherwise abnormally developed lianes. The cambium ring of the Bignoniaceae, after performing for a time its normal functions, begins, at certain points, to give off internally only a very small quantity of wood, and externally a correspondingly large amount of bast. As a result of this, deep wedges of irregularly-widening bast project into the outer so-called PERIAXIAL WOOD (Fig. 212). The originally complete cambium becomes thereby broken into longitudinal bands, which are broader in front of the projecting wood than at the apices of the bast wedges. As the periaxial wood is always developed from the

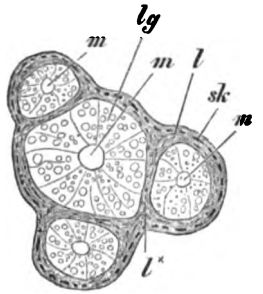


FIG. 211.—Transverse section of the stem of *Serjania Laruotteana*. *sk*, Part of the ruptured sclerenchymatous ring of the pericycle; *l* and l^s, bast zones; *lg*, wood; *m*, medulla. (× 2. After STRASBURGER.)

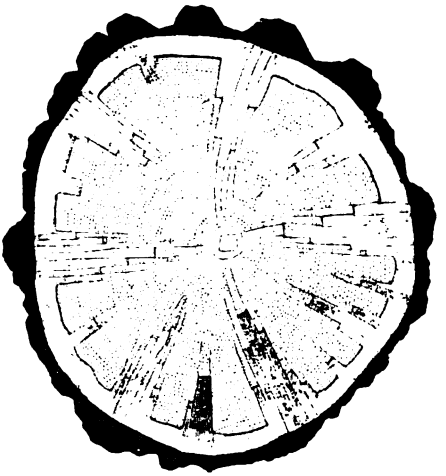


FIG. 212.—Transverse section of the stem of one of the Bignoniaceae. (Nat. size. After SCHENCK.)

inside and the wedges of bast from the outside of their respective cambium bands, they extend past each other without forming any lateral connection. Several woody cylinders are found in a number of tropical lianes belonging to *Serjania* and *Paullinia*, which are genera of the Sapindaceae. This anomalous condition arises from the unusual position of the primary vascular bundles, which are not arranged in a circle but form a deeply-lobed ring; so that, by the development of interfascicular cambium, the cambium of each lobe is united into a separate cambium ring. Each of these rings, independently of the others, then gives rise to wood and bast (Fig. 211).

2. Epiphytes ([90]).—In another group of cormophytes the leaves obtain stronger light by the plants being able to establish themselves on the stems and branches of high trees instead of being rooted in the ground. Such plants are termed epiphytes. Since the trees only afford them support they may be replaced by inorganic substrata such as rocks. The supply of the requisite water and nutrient salts will evidently be a difficulty. Consequently special adaptations are found to meet this; in many epiphytes shoot-tubers serve for water storage

(*e.g.* in the Orchidaceae), being replenished in moist periods, or there may be adaptations to catch water more directly.

In our latitudes epiphytes are represented only by some Algae, Lichens, and Bryophyta growing on the bark of trees. In the tropics, however, owing to the humidity of the atmosphere and the frequent and heavy downpours of rain, many cormophytes live as epiphytes. These plants, which belong especially to the Pteridophyta and the families Orchidaceae, Bromeliaceae, and Araceae, have no connection with the water-supply in the soil.

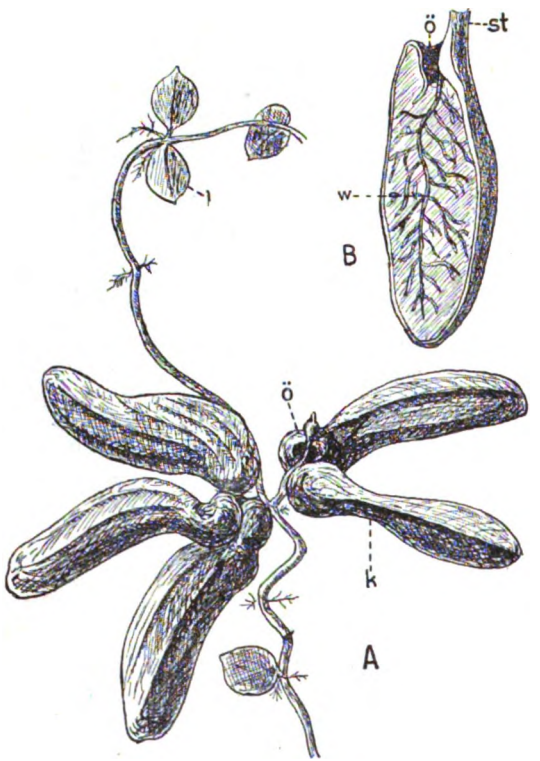


FIG. 213.—*A*, *Dischidia Rafflesiana* with foliage leaves (*l*) and pitcher leaves (*k*). *B*, Pitcher cut longitudinally; *ö*, opening; *st*, stalk; *w*, root. (*A* about ½, *B* about ⅓ nat. size. After TREUB.)

Their difficulty in obtaining water explains why the tropical epiphytes are nearly all well-marked xerophytes (Fig. 201). They are fastened by ATTACHING ROOTS which are relatively short, unbranched, and negatively heliotropic, and grow round and clasp the branch on which the plant grows. In addition to these attaching roots, much longer ABSORBENT ROOTS are found in many Araceae, hanging down freely in the air without branching until they reach the soil. Most epiphytes, however, are dependent on the rainfall for their water-supply, and frequently have special arrangements for collecting and retaining this. The many-layered epidermis of the aerial roots of many Orchids, and of various Aroids, undergoes a peculiar modification and forms the so-called VELAMEN, a parchment-like sheath surrounding the roots, and often attaining a considerable thickness. The cells of this enveloping sheath are generally provided with spiral or reticulate thickenings, and lose their living contents. They then become filled with either water or air, depending upon the amount of moisture contained in the surrounding atmosphere. These root-envelopes absorb water like blotting-paper; when the velamen is filled with water the underlying tissues impart a greenish tint to the root; but if it contains only air the root appears white. In other epiphytic Orchidaceae and Araceae there are upwardly-directed roots forming a branched

network in which falling leaves, etc., are caught and transformed into humus that retains moisture. Among the Ferns also there are epiphytes which collect humus by means of their leaves. In *Asplenium nidus* the leaves form a rosette enclosing a funnel-shaped cavity above the summit of the stem, and humus accumulates in this. In species of *Polypodium* and *Platycerium* special pocket-leaves and mantle-leaves serve for the accumulation of humus and water. The transformation of the leaves of the Asclepiadaceous plant *Dischidia rafflesiana* (Fig. 213) goes still further. Some of the leaves form deep pitchers with narrow mouths in which the water of transpiration becomes condensed; roots which branch freely grow into the pitchers, and obtain not only water but valuable nitrogenous substances. The pitchers are, in fact, usually tenanted by colonies of ants, and their excreta and remains form a source of food to the plant.

The American Bromeliaceae afford an extreme type of epiphytic plants in which the roots may be completely wanting (*e.g. Tillandsia usneoides*) or serve for attachment only. The absorption of water is entirely by means of peculiar, expanded, peltate hairs borne on the leaves. In many of these plants water collects in the cavities formed by the closely associated leaf-bases, and the plants are spoken of as CISTERN EPIPHYTES.

(c) Adaptations of Green Cormophytes to special Modes of Nutrition

The so-called INSECTIVOROUS or CARNIVOROUS PLANTS must be referred to here (91). These are plants provided with arrangements for the capture and retention of small animals, especially insects, and for the subsequent solution, digestion, and absorption of the captured animals by means of enzymes. All these

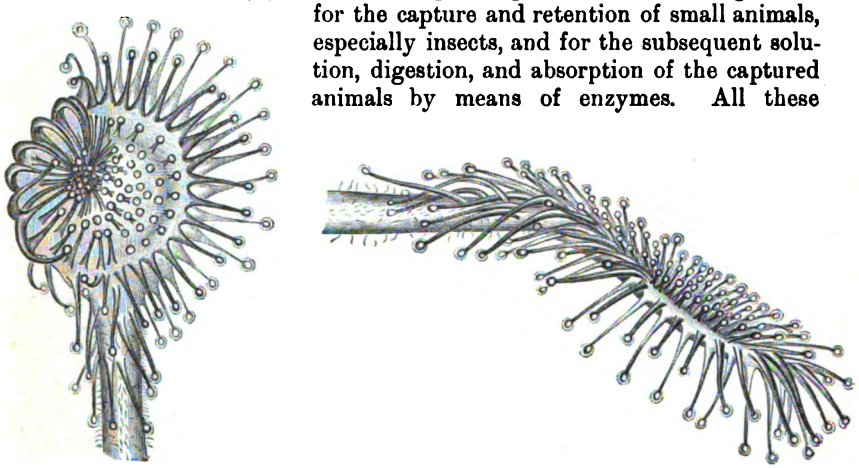


FIG. 214.—Leaves of *Drosera rotundifolia*. That on the left with its partly incurved tentacles is viewed from above, that on the right with expanded tentacles from the side. (× 4. After DARWIN.)

insectivorous plants are provided with chlorophyll, and can thus live autotrophically.

A great variety of contrivances for the capture of insects are made use of by carnivorous plants. The leaves of *Drosera* are covered with

stalk-like outgrowths ("tentacles"), the glandular extremities of which discharge a viscid acid secretion (Figs. 214, 215). A small insect which comes in contact with any of the tentacles is caught in the sticky secretion, and in its ineffectual struggle to free itself only comes in contact with other glands and is even more securely held. Excited by the contact stimulus, all the other tentacles curve over and close upon the captured insect, while the leaf-blade itself becomes concave and surrounds the small prisoner more closely.

In *Pinguicula* it is the leaf margins which fold

FIG. 215. — Digestive gland from *Drosera rotundifolia*. (× 60. After STRASBURGER.)

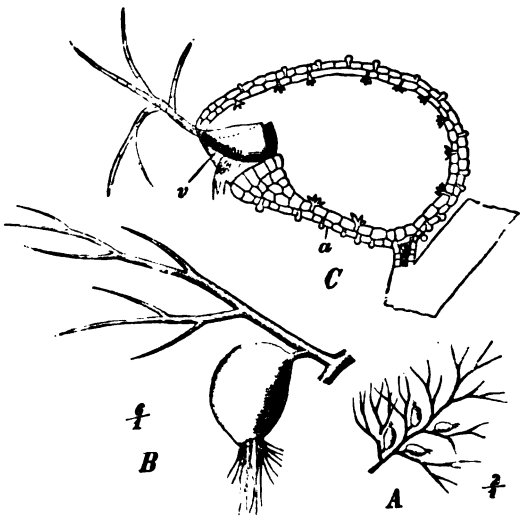


FIG. 216. — *Utricularia vulgaris*. *A*, Part of leaf with several bladders (× 2). *B*, Single pinnule of leaf with bladder (× 6). *C*, Longitudinal section of a bladder (× 28); *v*, valve; *a*, wall of bladder. (*A*, *B*, after SCHENCK; *C*, after GOEBEL.)

over any small insects that may be held by the minute epidermal glands. In species of *Utricularia* (Fig. 216), which grow frequently in stagnant water, small green bladders (metamorphosed leaf-segments) are found on the dissected leaves. In each bladder there is a small quadrangular opening closed by an elastic valve, which only opens inwards. Small crustaceans can readily pass through this opening, but their egress is prevented by the trap-like action of the valve, so that in one bladder as many as ten or twelve crustaceans will often be found imprisoned at the same time. The absorption of the disorganised animal remains seems to be performed by forked hairs which spring from the walls of the bladder.

More remarkable still, and even better adapted for its purpose, is

the mechanism exhibited by some exotic insectivorous plants. In the case of Venus's fly-trap (*Dionaea*), growing in the peat-bogs of North Carolina, the capture of insects is effected by the sudden closing together of the two halves of the leaf, which are fringed with long bristles. Fig. 217 shows a leaf of *Dionaea* in the expanded condition, ready for the capture of an insect. The European water-plant *Aldrovanda* has similarly-formed leaves.

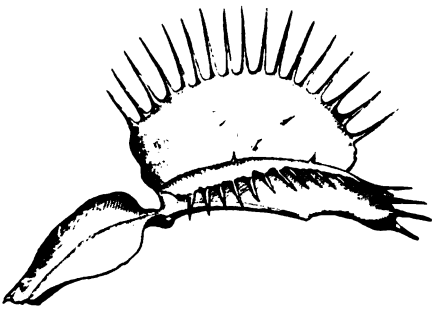


FIG. 217.—A leaf of *Dionaea muscipula*, showing the sensitive bristles on its upper surface, which, in the parts shaded, is also thickly beset with digestive glands. (× 4. After DARWIN.)

FIG. 218.—*Nepenthes robusta*. (⅛ nat. size. After SCHENCK.)

FIG. 219.—Pitchered leaf of a *Nepenthes*. A portion of the lateral wall of the pitcher has been removed in order to show the digestive fluid (*F*), excreted by the leaf-glands. (⅛ nat. size. After NOLL.)

In the case of other well-known insectivorous plants (*Nepenthes*,

Cephalotus, *Sarracenia*, *Darlingtonia*), the traps for the capture of animal food are formed by the leaves which grow in the shape of pitchers (Figs. 218, 219). The leaves of *Nepenthes*, for example, in the course of adaptation to the performance of their special function, have acquired the form of a pitcher with a lid which is closed in young leaves, but eventually opens. The pitcher, as GOEBEL has shown, arises as a modification of the leaf-blade. At the same time the leaf-base becomes expanded into a leaf-like body, while the petiole between the two parts sometimes fulfils the office of a tendril. These trap-like receptacles are partially filled with a watery fluid excreted from glands on their inner surfaces. Enticed by secretions of honey to the rim of the pitcher (in the case of *Nepenthes*), and then slipping on the extraordinarily smooth surface below the margin, or guided by the downwardly-directed hairs, insects and other small animals fall into the fluid.

B. Heterotrophic Cormophytes (92)

The green cormophytes utilise the light and by means of their chlorophyll construct organic substance from carbon dioxide and water; they also require to transpire in order to accumulate the nutrient salts from the soil in sufficient amount. Besides these forms others, which obtain some or all of their organic substance directly from the environment, are met with among cormophytes just as they occur among the thalloid plants. They do not depend upon light or transpiration, and frequently live at the expense of other living organisms as PARASITES. The peculiar form of these plants and the contrast they present to the green cormophytes are related to their special mode of nutrition. From the changes in their external appearance it is evident how far-reaching is the influence exercised by the chlorophyll. With the diminution or complete disappearance of chlorophyll, and consequent adoption of a dependent mode of life, the development of large leaf-surfaces, so especially fitted for the work of assimilation and transpiration, is discontinued. The leaves shrink to insignificant scales, or are completely wanting. The stems also are greatly reduced and, like the leaves, have a yellow instead of a green colour. Since there is no active transpiration the roots in many forms are reduced. Consequently the xylem portion of the vascular bundle remains weak, and secondary wood is feebly developed. In contrast to these processes of reduction resulting from a cessation of assimilation, there is the newly-developed power in the case of parasites to penetrate other living organisms and to deprive them of their assimilated products.

Many exotic parasitic plants, especially the Rafflesiaceae, have become so completely transformed by their parasitic mode of life that they develop no apparent vegetative body at all, and do not show the

characteristic segmentation of cormophytic plants, but grow altogether within their host plant, whence they send out at intervals their extraordinary flowers. In the case of *Pilostyles*, a parasite which lives on some shrubby Leguminosae, the whole vegetative body is broken up into filaments of cells which penetrate the host plant like the mycelium

FIG. 220.—Branch of a leguminous plant from the surface of which the flowers of a parasitic plant (*Pilostyles Ulei*, Solms) are protruding. (From GOEBEL'S *Organography*.)

of a fungus. The flowers alone become visible and protrude from the stems and leaf-stalks of the host plant (Fig. 220). The largest known flower, which attains a diameter of 1 metre, is that of the Sumatran parasitic plant *Rafflesia Arnoldi*; it is seated immediately on the roots of its host plant, which is a species of *Cissus*.

Cuscuta europea (Fig. 221), a plant belonging to the family of the Convolvulaceae, may be cited as an example of a parasitic Phanerogam. Although, owing to the possession of chlorophyll, it seems to some extent to resemble normally assimi-

lating plants, the amount of chlorophyll present is in reality so small that it is evident that *Cuscuta* (Dodder) affords an example of a very complete parasite.

The embryonic *Cuscuta* plantlet, coiled up in the seeds, pushes up from the ground in the spring, but even then it makes no use of its cotyledons as a means of nourishment; they always remain in an undeveloped condition (Fig. 221 at the right). Nor does any underground root-system develop from the young rootlet,

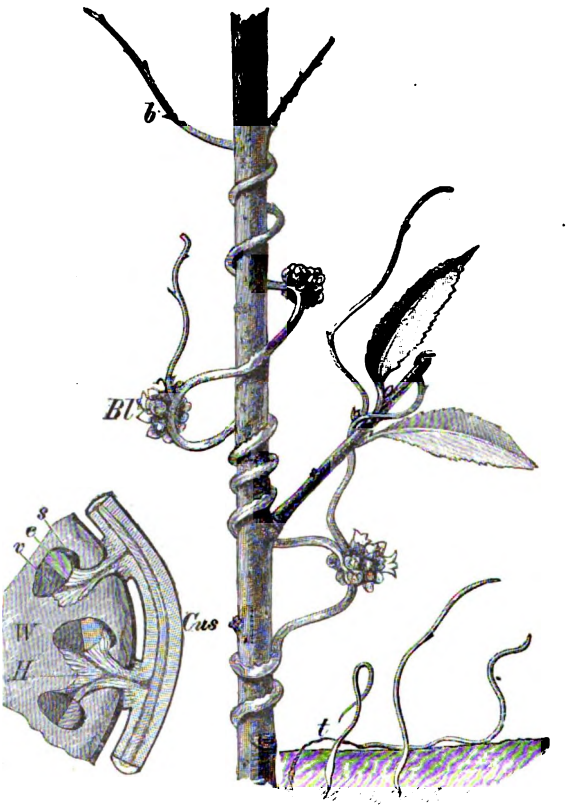


FIG. 221.—*Cuscuta europaea*. On the right, germinating seedlings. In the middle, a plant of *Cuscuta* parasitic on a Willow twig; *b*, reduced leaves; *Bl*, flower-clusters. On the left, cross-section of the host plant *W*, showing haustoria *H* of the parasite *Cus*, penetrating the cortical parenchyma and in intimate contact with the xylem *v* and the phloem *c* of the vascular bundles; *s*, displaced cap of sheathing sclerenchyma. (After NOLL.)

which soon dies off. The seedling becomes at once drawn out into a long thin filament, the free end of which moves in wide circles, and so inevitably discovers any plant, available as a host, that may be growing within its reach. In case its search for a host plant is unsuccessful, the seedling is still able to creep a short distance farther at the expense of the nourishing matter drawn from the other extremity of the filament, which then dies off (*t*) as the growing extremity lengthens. If the free end, in the course of its circling movements, comes

ultimately into contact with a suitable host plant, such as, for example, the stem of a Nettle or a young Willow shoot (Fig. 221 in the centre), it twines closely about it like a climbing plant. Papillose protuberances of the epidermis are developed on the side of the parasitic stem in contact with the host plant, and pierce the tissue of the host. If the conditions are favourable, these PRE-HAUSTORIA are soon followed by special organs of absorption, the HAUSTORIA (*H*). These arise from the internal tissues of the parasite, and possess, in a marked degree, the capability of penetrating to a considerable depth into the body of the host plant. They invade the tissues of the host, apparently without difficulty, and fasten themselves closely upon its vascular bundles, while single hypha-like filaments produced from the main part of the haustoria penetrate the soft parenchyma and absorb nourishment from the cells. A direct connection is formed between the xylem and phloem portions of the bundles of the host plant and the conducting system of the parasite, for in the thin-walled tissue of the haustoria there now develop both wood and sieve-tube elements, which connect the corresponding elements of the host with those of the parasitic stem (Fig. 221 at the left). Like an actual lateral organ of the host plant, the parasite draws its transpiration water from the xylem, and its plastic nutrient matter from the phloem of its host.

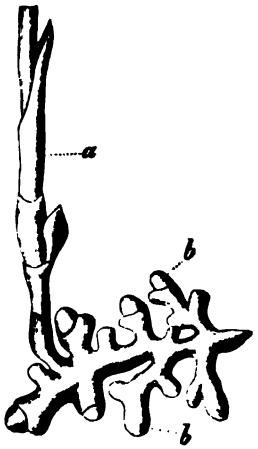


FIG. 222.—Rhizome of *Corallorrhiza innata*. *a*, Floral shoot; *b*, rudiments of new rhizome branches. (Nat. size. After SCHACHT.)

The seeds of *Orobanche* (Broom rape), another parasite, only germinate when in contact with the roots of the host plant; only its haustoria penetrate the roots, and its light yellow, reddish-brown, or amethyst-coloured flower-shoot appears above the surface of the ground. *Orobanche* (Fig. 764), like *Cuscuta*, contains a small amount of chlorophyll. Both are dreaded pests; they inflict serious damage upon cultivated plants, and are difficult to exterminate.

A similar appearance to *Orobanche* is presented by some plants which grow in the humus soil of woods, and are, therefore, not at first sight regarded as parasites: certain Orchids (*Neottia*, *Coralliorrhiza*, *Epipogon*) and *Monotropa*. The absence of chlorophyll, the reduction of the leaves to scales, and (in *Coralliorrhiza*) the absence of roots also (cf. Fig. 222), are indications that these plants obtain organic material from without. They cannot themselves directly utilise the humus, but fungi, which obtain food from this, are harboured in their subterranean parts as a MYCORRHIZA. A proportion of the fungal hyphae is later digested by the plant. These cormophytes are thus in a sense parasitic on the fungi of the humus.

In contrast to these parasites, which have come to be almost entirely dependent on other plants for their nourishment, there are others which, to judge by external appearance, seem to have a high degree of independence, since they possess large green leaves and are capable of assimilation. They are, however, parasitic, since they can only develop normally, when their roots are connected by means of haustoria with the roots of other plants; they are spoken of as PARTIAL PARASITES. *Thesium* belonging to the Santalaceae, and the following genera of the Rhinanthaceae, *Rhinanthus*, *Euphrasia*, *Pedicularis*, *Bartsia*, *Melampyrum* and *Tozzia*, may be mentioned as examples; in *Tozzia* the parasitism is especially well marked in the earliest developmental stages.

The Mistletoe (*Viscum album*), belonging to the Loranthaceae as do many similarly parasitic exotic forms, possesses good-sized leaves, but reduced roots; it is so well provided with chlorophyll as to be able to manufacture all the carbohydrates it requires.

II. Organs of Reproduction ([93])

A. Significance of Reproduction to the Organism.—A natural or an accidental death is the end of every organism. For the maintenance of living beings reproduction is thus as essential as nutrition. The main feature of reproduction lies in portions of an individual continuing after its death, with the power of developing into new individuals. On account of the possibility of accidental death, reproduction takes place before this occurs naturally, and usually involves the formation of special germs, which separate from the parent plant and, repeating the development of this, grow into new individuals.

In most plants a division of labour is apparent between the vegetative and reproductive organs. This becomes more striking in the more highly organised forms, in which an increasing number of parts co-operate in reproduction.

B. General Properties of the Germs.—The construction of the germs, as in the case of the vegetative organs, is closely connected with the purposes they have to serve.

The small size of most reproductive bodies, in comparison to the vegetative organs, is characteristic. The parent plant can thus produce numerous germs without excessive expenditure of material, while at the same time the distribution of the germs is facilitated.

The object of reproduction is not merely the production of a new individual in place of the parent, but an increase in the number of individuals. Since the majority of the germs may not meet with favourable conditions for their germination and growth, and a large number will perish before they can in turn reproduce, the production of only a single germ would result in the speedy extinction of the species. An apparently prodigal production of germs is thus the rule. A cap-fungus or a fern may form millions of spores; a poplar tree, according to BESSEY, may ripen twenty-eight million seeds annually.

Provision is further necessary for the separation of the germs from the parent and their dispersal widely from it. In the immediate neighbourhood there may not be the conditions for germination, or there may be no room for the development of the progeny.

Lastly, it is necessary for the germs to be provided with reserve food materials from the parent organism, in order that their development, until they are able to nourish themselves, should be ensured.

Frequently the reproductive bodies serve to carry the organism over cold or dry periods that are unfavourable to active life. They

pass into a resting condition (p. 305), in which they are more resistant to injurious influences (desiccation, frost, heat). Such germs are usually thick-walled, and only germinate on the return of favourable conditions.

C. Types of Reproductive Bodies.—The germs which can develop into plant bodies composed of many cells may themselves be unicellular (spores) or multicellular (gemmae and seeds). Both kinds may be produced irregularly on the plant, or be restricted to definite regions, which are specially constructed for reproduction, and exhibit great variety. These differences are of primary importance for the division of plants into classes, orders, families, etc. Two types of reproduction are readily distinguished in plants of nearly all the classes of the vegetable kingdom.

In the first type, cells or multicellular bodies are formed which can develop into a new independent individual on their separation from the parent, either at once or after a period of rest. This kind of reproduction is termed VEGETATIVE, ASEXUAL, or MONOGENETIC.

In SEXUAL REPRODUCTION, the second of the two modes of reproduction, two kinds of reproductive cells, each of which carries the characters of the organism producing it, are formed, but neither is directly capable of further development, and both perish in a very short time, unless opportunity is given for their fusion with each other. Not until the one cell has fused with the other cell does the product acquire the capacity of development and growth. This mode of reproduction is termed SEXUAL or DIGENETIC reproduction.

Most plants have both methods of reproduction. Sexual reproduction is wanting only in the lowest groups (the Bacteria, Cyanophyceae, and some Algae and Fungi). Some plants have several methods of asexual reproduction.

In certain exceptional cases a sexual cell may proceed to develop further without fertilisation. This is termed PARTHENOGENESIS (94). This has been found in the vegetable kingdom in *Chara crinita*, one of the Algae, and in the development of the embryo from the unfertilised ovum in a number of families of higher plants (Compositae, Ranunculaceae, Rosiflorae, Thymeleaceae, Urticaceae), and in the Marsiliaceae.

The process of fertilisation of sexual cells may, in particular cases, be replaced by the fusion of the nuclei of adjoining vegetative cells (95). This is the case in the prothallium of certain cultivated forms of Ferns (*e.g.* of *Dryopteris* (*Lastraea*) and *Athyrium*). The product of this fusion effects the reproduction, the sexual organs of the prothallium being reduced.

D. Alternation of Generations (96).—In plants there is frequently an alternation of two generations differing in their modes of reproduction; these may be morphologically distinct and independent individuals. The life-history of such a plant is thus composed of

two kinds of individuals, which regularly alternate with one another, are frequently very different in form and structure, and bear different reproductive organs. The reproduction of the one generation (sporophyte) is asexual; that of the other (gametophyte) is sexual. The Fern may be taken as a typical example. The leafy fern plant is the sporophyte, and produces only asexual spores. The spore on being shed does not grow into a new fern plant, but into a small thalloid structure known as the prothallium (Fig. 97), which is the gametophyte, and reproduces sexually. The fertilised egg-cell develops into a leafy fern plant. The reproductive cells of the one generation give rise to the other generation, and there is thus a regular alternation of the sporophyte and gametophyte. The two generations may, however, as in the case of the Brown Alga, *Dictyota*, resemble one another.

Frequently the two generations are not represented by independent individuals, but the one remains permanently connected to the other like a parasite on its host plant. Careful investigation may then be required to establish the existence of an alternation of generations. This is the case for the Bryophyta and the Seed-plants.

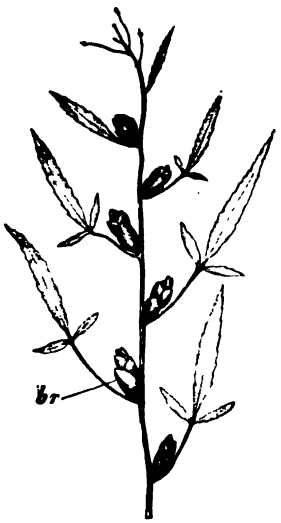


FIG. 223.—Shoot of *Dentaria bulbifera*, bearing bulbils, *br*. (Nat. size. After SCHENCK.)

Both generations may be able to reproduce their like by vegetative reproduction. Multicellular gemmae formed on the prothalli of some ferns grow into new prothalli; on the fern plant bulbils, which grow into new leafy plants, may be produced.

1. Multiplication by Multicellular Vegetative Bodies (Budding)

This occurs in many Bryophyta, *e.g.* in *Marchantia*, where the gemmae are formed in special receptacles on the thallus (Figs. 444, 445). It is also widely spread in the form of budding in Pteridophyta and Phanerogams.

Specially-formed lateral shoots serving to reproduce the plant are seen in the runners or stolons produced above or below ground by many plants. The RUNNERS of the Strawberry are slender cylindrical branches from the axils of the leaves of the rosette; they root from the terminal bud, which becomes independent by the subsequent decay of the runner. Many BULBS and TUBERS serve for reproduction in the higher plants, as do also BULBILS (Fig. 223) and the winter buds which become detached as the HIBERNACULA of a number of aquatic plants (*e.g. Hydrocharis*, *Stratiotes*).

Buds may also arise in places where no growing points are normally present; they are then adventitious. Such buds are most commonly found on leaves,

sometimes on the leaf-blade, *e.g.* in the notches of the leaf margin in *Bryophyllum*, and on the leaves of *Cardamine pratensis*. The leaves of *Begonia*, *Drosera*, etc., only produce buds after they have been separated from the plant.

Many herbaceous perennials, without forming special organs of vegetative reproduction, increase in number of individuals by the decay of the older portions of their branched rhizomes isolating the branches. Among Sea-weeds also the mechanical action of the surf may separate portions of the thallus which can grow into new thalli. *Caulerpa* is propagated in this fashion.

2. The Formation of Reproductive Cells

(a) Asexual Reproductive Cells (Spores). — Many unicellular Thallophyta (Flagellata, Bacteria, Cyanophyceae, Diatomeae) are multiplied vegetatively by dividing into two, the daughter cells separating from one another. In others, such as the Protococcaceae, the protoplast within its wall divides into several or many daughter protoplasts; these separate from one another and emerge from the parent cell through a pore or split in the cell wall. The unicellular organism in these cases has at the period of reproduction become converted into a receptacle containing the germ cells, or a SPORANGIUM; the germ cells which give rise to daughter organisms may be termed ENDOSPORES or SPORANGIAL SPORES.

Among the multicellular Thallophytes simply-organised forms are met with that might be regarded as cell colonies, in which the body sometimes dissociates into the individual cells; these then serve for vegetative multiplication. In other forms the protoplasts of all the cells, usually after preliminary division into daughter protoplasts, emerge at the period of reproduction from the cells which have thus become sporangia.

The more highly organised multicellular Thallophyta exhibit a division of labour, only some portions or cells, which often have a definite structure and position on the thallus, producing asexual reproductive cells. Such spore-producing parts are often united in numbers to form fructifications of more complex structure.

Thus in many Fungi the hyphae concerned in reproduction become associated within the soil into more or less massive and variously-shaped FRUCTIFICATIONS which later emerge to the surface.

The mode of origin of the spores is similar in the higher and lower forms. In many Fungi germ cells are isolated by budding and constriction from certain hyphae as EXOSPORES or CONIDIOSPORES (Fig. 224). In other Fungi and in the majority of the Algae the asexual cells originate as ENDOSPORES or SPORANGIAL SPORES from the protoplasts of certain cells (SPORANGIA), and emerge through openings in the wall of this (Figs. 225, 231 *sp*).

The asexual spores of the Thallophyta are in part adapted to distribution by means of water, as in the case of many sporangial spores of Algae and Fungi. These spores are naked, without a cell

wall, and as a rule able to move through the water by the aid of cilia (Figs. 225, 229 *A*). They are termed SWARM SPORES or ZOOSPORES, and the receptacles in which they are formed are spoken of as ZOOSPORANGIA (Green and Brown Algae, some Phycomycetes).

The spores in other Thallophyta are adapted to dispersal by wind. Examples are afforded by many sporangial spores and all conidiospores of the Fungi. They are very small and light, surrounded by thick walls and resistant to drying. Such spores are usually produced by organs which are exposed to the air; in Fungi living in or on solid substrata they may be borne on aerial hyphae (Fig. 224). They are thus borne on CONIDIOPHORES or SPORANGIOPHORES or on FRUCTIFICATIONS.

FIG. 224.—Conidiophore of *Aspergillus herbariorum*. (× 540. After KNY.)

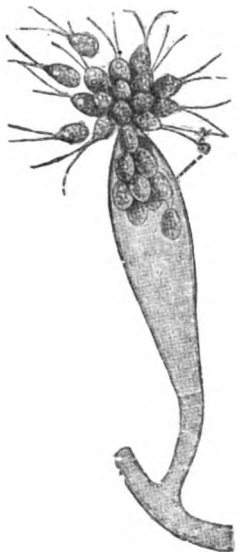


FIG. 225.—*Saprolegnia mixta*. Sporangium from which the biciliate zoospores (*sp*) are escaping. (After G. KLEBS.)

In the **Bryophyta, Pteridophyta,** and **Spermatophyta** the asexual cells are always developed as endospores in special sporangia of more complicated structure than in the Thallophyta. These sporangia are multicellular structures, one or more outer layers of cells forming the wall, and the enclosed cells constituting the sporogenous tissue (Fig. 226 *sg*). When ripe, the sporangia have usually special arrangements in the wall for opening and shedding the small and light spores, which may be dispersed by wind or (in the case of many Spermatophytes) by animals. The spores are always surrounded by cell walls.

The spore capsules or SPOROGONIA of the Bryophyta attain the most complicated structure. They are as a rule stalked and are situated on the thallus or at the ends of leafy branches. The sporo-

gonium is not, as appears at first sight, a member of the moss-plant, but lives on this like a parasite. It is, in fact, the spore-bearing generation (sporophyte) which remains permanently attached to the moss-plant (gametophyte).

In the Pteridophyta, on the other hand, the leafy plant is the sporophyte and bears small and inconspicuous sporangia, usually on leaves which are termed SPOROPHYLLS. These may resemble the foliage leaves, but there is often a division of labour between the sporophylls and the foliage leaves. The former are devoted mainly or entirely to the production of sporangia and, therefore, differ from the foliage leaves in the lack of expanded green surfaces. The sporophylls are often associated in numbers at the ends of branches of

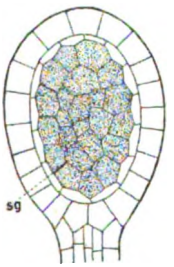


FIG. 226. — Diagram of the sporangium of a Pteridophyte, the sporogenous tissue (*sg*) being enclosed by a sterile wall.

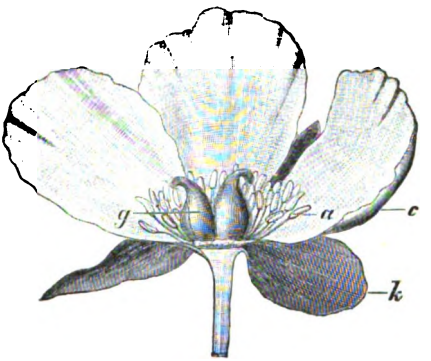


FIG. 227.—Flower of *Paeonia peregrina*. *k*, Calyx; *c*, corolla; *a*, stamens; *g*, carpels. The nearer sepals, petals, and stamens are removed to show the pistil formed of two free carpels. (½ nat. size. After SCHENCK.)

limited growth, as in *Equisetum* and *Lycopodium* (cf. Figs. 486, 491). These differ in appearance from the vegetative shoots and die off after they have served for reproduction. They are known as CONES or FLOWERS. THE SIMPLEST FLOWER IS THUS A PORTION OF A SHOOT WHICH BEARS SPOROPHYLLS. The cones of Pteridophyta may have a number of sterile scale leaves at the base.

In the Spermatophyta the sporangia are also formed in special regions of the shoot or FLOWERS, all the members of which are concerned with reproduction and not with the nutrition of the plant. These flowers, which are homologous with those of the Pteridophyta, are metamorphosed regions of the foliage shoots. They are the ends of long or short shoots, the leaf primordia of which do not become foliage leaves but develop as the crowded floral leaves. These have the diverse forms of SEPALS, PETALS, STAMENS, and CARPELS.

The STAMENS produce the pollen or POLLEN GRAINS in the POLLEN SACS, which are special sporangia with a many-layered wall. The

pollen grains are spores (Fig. 32) which to begin with are single cells but later become multicellular (Gymnosperms), or at least contain more than one nucleus (Angiosperms). The CARPELS, which are free in the Gymnosperms but form closed OVARIES in the Angiosperms, bear the OVULES. These are shortly-stalked oval bodies of complicated structure. In each ovule a single spore is permanently enclosed, protected by the sterile integuments.

The cone-like flowers of the Gymnosperms ([97]), composed of numerous, spirally-arranged, scale-like stamens or carpels, closely resemble the cones of the Pteridophyta. The flowers of the Angiosperms ([97]) have usually a quite distinct appearance (Fig. 227) owing to (1) the limited number of the usually whorled floral leaves, (2) the frequent differentiation of the outer floral leaves into firm green sepals and coloured delicate petals, (3) the characteristic form of the stamens, and (4) the union of the carpels to form the pistil. All these parts of the flower are arranged regularly. In the typical angiospermic flower, five whorls, each of five floral leaves, regularly alternate (Fig. 228); the outermost whorl is formed of the sepals which enclose and protect the other parts when young, the second is formed of the petals, the third and fourth of the stamens, and the fifth and highest by the carpels ([98]). These foliar structures arose from the shortened, and often flattened or hollowed, floral axis; they are often united with one another and with the axis in such a way as to require thorough comparative and developmental study to ascertain the facts clearly.

FIG. 228.—Diagram of a Liliaceous flower. The main axis is indicated by a black dot, opposite to which is the bract. (After STRASBURGER.)

(b) Sexual Reproductive Cells. Gametes. 1. Different Forms of Sexual Cells and Sexual Organs.—A great variety in the methods of sexual reproduction is shown by plants; different as the extremes are, however, they are connected by intermediate links.

Thallophyta.—In many of the lower Algae and Fungi all the cells of the plant may simultaneously form sexual cells. With progressive organisation a division of labour is met with. As in the case of the formation of asexual reproductive cells, certain cells or organs with definite positions carry on the sexual reproduction. The parts of the plant body which bear the sexual organs may be specialised in relation to this.

In the simplest types of sexual reproduction met with in the lower Algae and Fungi, the sexual cells or GAMETES are usually naked protoplasts of similar size and structure; these resemble the asexual swarm spores but conjugate with one another (ISOGAMY, Fig. 229 *B*). They develop, singly or in numbers, from the protoplasts

of certain cells termed GAMETANGIA, the process resembling the origin of the swarm spores. The product resulting from the conjugation of the gametes is called a ZYGOTE or ZYGOSPORE (Fig. 229 *B* 4). The facts are in favour of regarding the gametes as homologous with the swarm spores, from which they often differ only in their smaller size, and the gametangia as homologous with sporangia. By this is meant that the gametes and gametangia have been derived phylogenetically by the modification of swarm spores and sporangia. Such gametes are capable of active movement by means of cilia; they seek one another in the water and unite in pairs (Fig. 229 *B*).

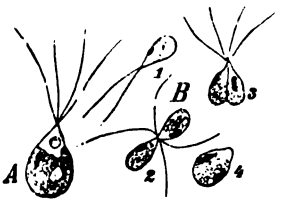


FIG. 229.—*Ulothrix zonata*. *A*, Asexual swarm spore; *B1*, a gamete; *B2*, *B3*, conjugating gametes; *B4*, zygote resulting from conjugation. (× 500. After STRASBURGER.)

The gametes, however, frequently differ in size in the Algae and Fungi; the larger gametes, which contain abundant reserve materials, are female (♀) and the smaller are male (♂). The female gamete may be non-motile when it is known as an egg-cell. In this case the small SPERMATOZOID seeks out and fertilises the large EGG-CELL (OOGAMY). In the case of oogamy the gametangia are usually

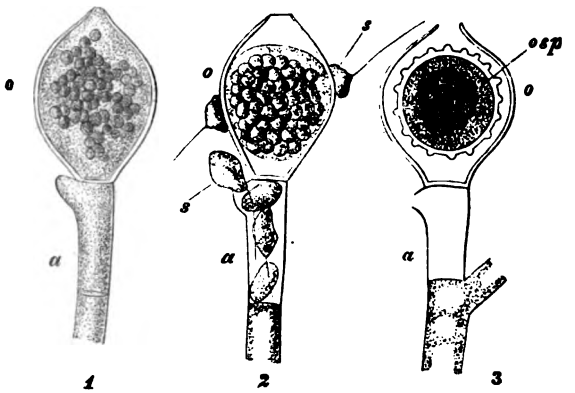


FIG. 230.—*Monoblepharis sphaerica*. End of filament with terminal oogonium (*o*) and an antheridium (*a*). 1. Before the formation of the egg-cells and spermatozoids. 2. Spermatozoids (*s*) escaping and approaching the opening of the oogonium. 3. *osp*, ripe oospore, and an empty antheridium. (× 800. After CORNU, from VON TAVEL, Pilze.)

different. The cells in which the small naked spermatozoids arise in large numbers are termed ANTHERIDIA (Figs. 230, 2 *a*; 231 *a*), while those within which one or more egg-cells are formed are the OOGONIA (Figs. 230, 2; 231 $o_{,}$, $o_{,,}$). The egg-cell (OOSPHERE), which is usually naked, frequently remains in the oogonium, in the wall of which an opening forms (Figs. 230, 2; 231 $o_{,}$, $o_{,,,}$ *ö*). Fertilisation of

the receptive oosphere results from spermatozoids, which have been liberated into the surrounding water in an actively motile condition, being chemotactically attracted by substances excreted from the egg-cells.

Numerous transitions between the two conditions show clearly that oogamy has been derived phylogenetically from isogamy. From this it follows that the antheridia and oogonia are homologous with one another, and also with the sporangia (cf. also Fig. 231).

It is not until after the entry of a spermatozoid that the egg-cell becomes capable, either at once or after a resting period, of developing further. As a rule, after becoming surrounded by a thick wall it separates from the parent plant as a unicellular oospore (Fig. 230, 3 *osp*), and only commences its independent development later with the bursting of its wall. In other cases, while still attached to the parent plant, it develops into a multicellular and more or less segmented body which produces unicellular asexual spores; these spores are then set free from the parent plant as the true reproductive bodies.

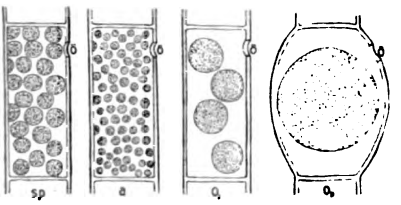


FIG. 231.—Diagrams founded on Algae. *sp*, Sporangium with spores; *a*, antheridium with spermatozoids; o_1, oogonium with several and o_{11} with a single egg-cell; *ö*, the pore in the cell wall.

Bryophyta, Pteridophyta.—Oogamy is the rule in these groups. The male and female sexual organs are of more complicated structure than in the Thallophyta. They are not single cells but have walls composed of a layer of sterile cells. In the case of the multicellular antheridia (Fig. 232, 1) this encloses a larger or smaller number of cells with abundant protoplasm (the SPERMATOGENOUS TISSUE), from each of which a spermatozoid will be formed. In the flask-shaped female sexual organ, which is known as an ARCHEGONIUM, there is only one egg-cell surrounded by the wall formed of a layer of cells (Fig. 232, 2). The archegonia and antheridia are homologous structures. They have special arrangements for opening at maturity. In the Bryophyta they are borne on the thalloid or leafy gametophyte. In the Pteridophyta the sexual organs are not borne on the leafy plant (which has been seen to be reproduced by spores) but on the prothallium, which is the sexual generation or gametophyte living independently of the sporophyte.

In the Bryophyta and Pteridophyta the oosphere after fertilisation, which takes place in the same way as in the Thallophyta, develops forthwith into the EMBRYO which becomes the SPOROPHYTE (the stalked capsule in Bryophyta, and the leafy plant in the Pteridophyta).

Spermatophyta.—In this group also the sexual reproduction is exclusively oogamous, but the sexual organs have come to differ

widely from the simpler types. The gametes are formed in greatly reduced or unrecognisable archegonia and antheridia; these are produced in extremely reduced prothallia, often consisting of only a few cells, that are enclosed in the pollen grains and ovules of the flowers. The pollen grains contain the male sexual cells, while one or more egg-cells are contained in the ovule.

The peculiar method of fertilisation in spermatophytes is connected with the fact that the egg-cell remains enclosed within the ovule in the flower. The pollen grains after being shed from the pollen sac require to be carried to the ovules in the case of Gymnosperms, or to a special receptive portion of the ovary called the STIGMA in the Angiosperms. This is the process of POLLINATION. Most of the manifold modifications of the flowers of Angiosperms are adaptations to the method of pollination (99), which always involves special means of transport of the pollen. When, as is often the case, male and female organs are present in the same flower, *i.e.* in hermaphrodite flowers, it might be assumed that no special arrangements would be necessary to bring the pollen to the stigma. More accurate investigation has, however, shown that such adaptations exist in abundance and are often of the most detailed nature. They do not simply aim at the conveyance of the pollen to the stigma of the same flower; often they render such SELF-POLLINATION (a'u'togamy) impossible and effect CROSS-POLLINATION (allogamy), *i.e.* the conveyance of pollen to the stigma of another flower on the same plant (geitonogamy) or on another individual (xenogamy). The transport of the pollen may be by wind, water, or the agency of animals attracted to the flowers by their colour, scent, or nectar; thus most flowers can be classed as ANEMOPHILOUS, HYDROPHILOUS, or ZOIDIOPHILOUS (cf. the Special Part). Most spermatophytes have thus become independent of the presence of water for the purpose of fertilisation and are in a special sense land plants.

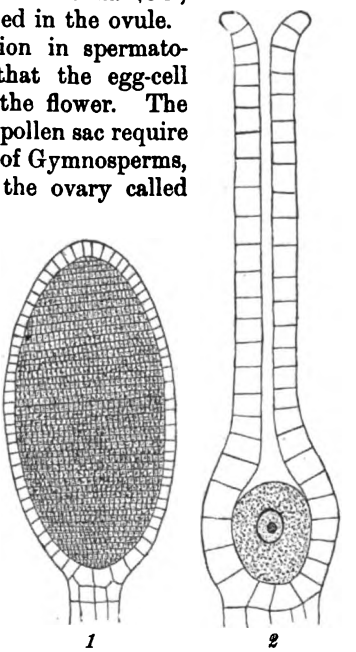


FIG. 232.—1. Antheridium, with wall of sterile cells enclosing the spermatogenous tissue. 2. Archegonium, with corresponding wall and an egg-cell. Both based on a Liverwort.

In addition to plants which show allogamy there are others which have arrangements leading to autogamy, either when cross-pollination does not succeed, or primarily as in cleistogamous flowers (cf. the Special Part).

After pollination the pollen grain grows out into a POLLEN TUBE,

which in Angiosperms makes its way by means of the style to the cavity of the ovary and through the outer layers of sterile cells of an ovule to the egg-cell. When an open connection has been established between the pollen tube and the egg-cell, the latter is fertilised by a nucleus from the pollen tube. The fertilised egg develops within the enlarging ovule to a multicellular embryo, which becomes segmented into the COTYLEDONS, RADICLE, and PLUMULE. The ovule becomes the SEED, the outermost tissues giving rise to the seed-coat. THE SEED, WHICH IS SHED WHEN RIPE AND SERVES TO MULTIPLY THE PLANT, IS THUS A FURTHER DEVELOPED OVULE ENCLOSING AN EMBRYO. The ovary also develops further after fertilisation and gives rise to the FRUIT. When this remains attached to the plant it opens when mature by splits, pores, or the separation of a lid, in order to liberate the seeds (capsule). Often the whole fruit enclosing the seed is separated from the plant, as in the case of berries, nuts, and stone-fruits.

The seeds or the detached fruits are adapted for dispersal ([100]) like other reproductive bodies. This is effected by the same means as the transport of pollen, by currents of air or water, by means of animals, and sometimes by special constructions or movements of the plant. The construction of seeds and fruits shows adaptation to the mode of dispersal (cf. the Special Part).

On the seeds being thus sown, GERMINATION ([101]) commences after a longer or shorter time. As a rule the root of the embryo emerges first, rupturing the seed-coat. Since this is often very hard, special regions for the exit of the root may be present in it (*e.g.* in the Coconut). In the further development of the shoot of the seedling, manifold differences become apparent in different kinds of plants; these will be described in the Special Part. The seedling at first grows at the expense of food materials provided by the parent plant and stored in the seed.

A peculiar type of asexual reproduction (apogamy) occurs in some flowering plants and replaces the sexual reproduction. Within the ovule and replacing the suppressed egg cell, asexual embryos are developed from other cells ([95]). The seeds thus include no product of sexuality but have become organs of vegetative reproduction. This formation of adventitious embryos is commonly associated with POLYEMBRYONY, *i.e.* the formation of a number of embryo plants in a single seed (*Funkia ovata*, *Citrus aurantium*, *Caelebogyne ilicifolia*, etc.).

2. The Process of Cell-Fusion in Fertilisation and its Results.—The actual process of fertilisation in its simplest form can be best observed in those lower organisms with similar gametes (Fig. 229). In these it can be easily shown that not only the cytoplasm of the two cells but sooner or later the nuclei also fuse. When the male cell possesses chromatophores, which in many Algae (Florideae, *Chara*, etc.) is not the case, they do not fuse with those of the female cell. They either coexist in the fertilised cell or, when a constant number

of chromatophores is maintained, disappear. In Angiosperms, so far as our present knowledge goes, only a male nucleus, without cytoplasm or chromatophores, enters the oosphere. From this it has been concluded THAT THE ESSENTIAL ELEMENT IN FERTILISATION IS THE PASSAGE OF THE MALE NUCLEUS INTO THE EGG-CELL.

In the typical process of nuclear division it has been seen that the nuclei of an individual possess a constant number of chromosomes characteristic of the species. The male gamete thus contributes as many chromosomes as the female gamete. These chromosomes do not fuse in the conjugation of the sexual nuclei, so that the nucleus of the zygote has double the number of chromosomes possessed by the sexual cells ([102]). It is DIPLOID and contrasts with the HAPLOID nuclei of the gametes.

The nuclei resulting from the further division of the nucleus of the zygote are as a rule diploid; in each there are as many chromosomes derived from the male as from the female nucleus. When the chromosomes of the haploid cells are characterised by differences in size which are apparent at each nuclear division, the diploid nuclei show pairs of chromosomes of each size. These chromosomes of equal length, the one derived from the male and the other from the female parent, as a rule lie in pairs in the nuclear plate (Fig. 14).

Since the nuclei of the sexual cells of all the individuals of a race are always haploid, while the conjugation nucleus and as a rule the products of its division are diploid, there must be a change from the diploid to the haploid condition at some point in the developmental history of the individual. Were this not so, the number of chromosomes would double with each generation. The change is effected at the REDUCTION DIVISION ([103]), which is a peculiar nuclear division in which there is a separation to form the daughter nuclei of entire chromosomes, and not half-chromosomes resulting from longitudinal splitting. This occurs at a definite point in the development, which, however, differs in different organisms. Thus a regular alternation of the haploid and diploid phases of the nucleus is characteristic of the ontogenetic development of sexual organisms.

Frequently, but not always, the alternation of nuclear phase is connected with the alternation of generations, as in many Algae, Fungi, the Bryophyta, Pteridophyta, and Spermatophyta. The sporophyte arising from the fertilised egg is diploid, and the reduction division precedes spore formation. As a result the spores, the gametophytes developed from them, and the sexual cells are haploid.

In many Algae, however, the first division of the nucleus of the zygote is the reduction division, so that all the cells of the organism, including the sexual cells, with the exception of the fertilised egg, are haploid. In others, such as *Fucus*, the reduction takes place at the formation of the sexual cells, so that the opposite case is presented of all the cells with the exception of the gametes being diploid.

There are certain remarkable cases in which the one generation develops from

the vegetative cells of the other without change in the number of chromosomes. In *Athyrium filix foemina clarissima*, Jones, the fern plant arises without nuclear fusion from vegetative prothallial cells with diploid nuclei; without any production of spores, or the occurrence of a reduction division, the diploid cells of the leaf margin produce diploid prothallia (APOSPORY). According to YAMANOUCHI (in *Nephrodium molle*) a haploid prothallial cell may, without nuclear fusion, give rise

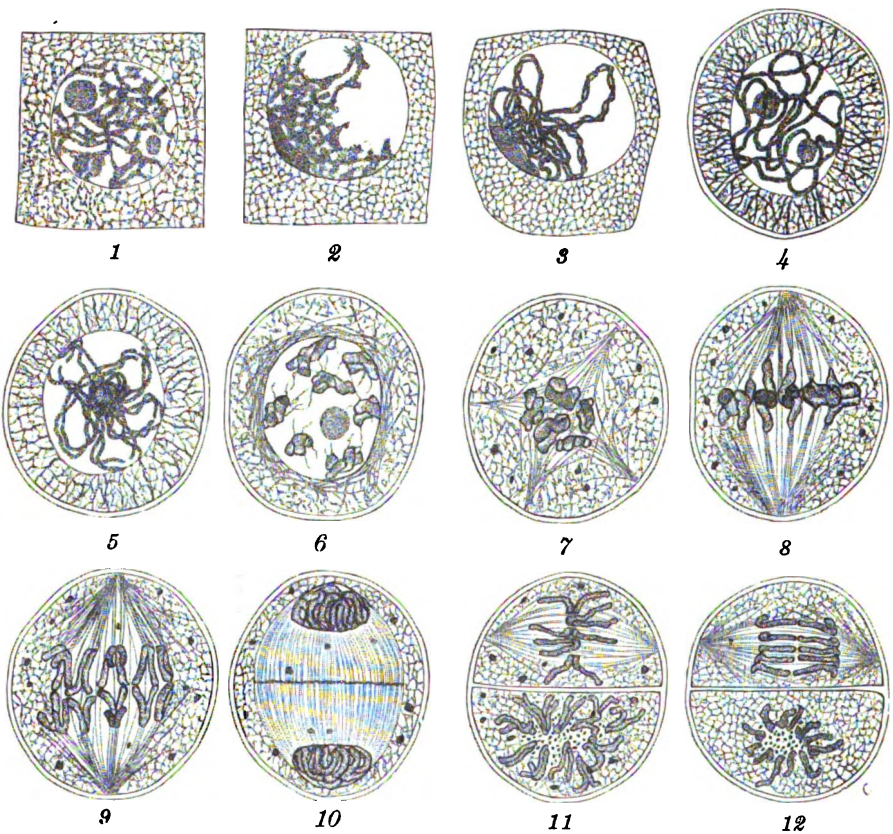


FIG. 233.—Pollen-mother-cell of a Lily in division, somewhat diagrammatic. Fixed with chrom-acetic acid and stained with iron haematoxylin. The chromatophores are not visible. 1. The separation of the chromosomes. Further description in text. (After STRASBURGER.)

to a haploid fern-plant. Further, it is possible to obtain experimentally, on the regeneration of cut portions of the stalks of moss capsules, a diploid moss plant, *i.e.* a diploid gametophyte; this produces diploid sexual cells that are capable of fertilisation. Tetraploid moss capsules are the result, and from these again by regeneration tetraploid moss plants have been obtained. It is evident, therefore, that there is not a direct connection between the chromosome number and the construction of the two generations (95).

In some plants the reduction division is omitted so that diploid egg-cells are

formed (95). Such eggs, which already have the double number of chromosomes usually only attained on fertilisation, proceed to develop without fertilisation. This is the case for the unfertilised egg-cells of the Spermatophyta, Marsiliaceae, and *Chara*, mentioned on p. 193, while in other Algae the haploid egg-cell develops parthenogenetically into a new plant. When diploid sexual cells proceed to develop without fertilisation, it is usual to speak of apogamy (cf. p. 202) and not of parthenogenesis.

The reduction division in contrast to the typical division is termed HETEROTYPIC, and is also spoken of as MEIOSIS. It is characteristic of this, that in the prophase the nuclear contents become for a period contracted together at one side, at least in fixed preparations (SYNAPSIS, Fig. 233, 2, 3). It is further characteristic of the succeeding stages that the paternal and maternal chromosomes become associated or united in pairs or GEMINI. The number of these GEMINI is half as great as the number of chromosomes in the tissue cells of the same plant, since two chromosomes are represented by each segment. The paired chromosomes become shorter and thicker and are distributed around the periphery of the nucleus; this is the condition that has been termed DIAKINESIS (5, 6). At this stage kinoplasmic filaments are becoming applied to the nuclear membrane (6); the latter disappears, and the nuclear spindle, which is at first multipolar (7) but ultimately becomes bipolar (8), originates from the kinoplasmic fibres. The paired chromosomes become attached to the fibres of the spindle and arranged in an equatorial nuclear plate (8). Shortly afterwards the separation of the chromosomes, until now united in pairs, takes place (9). IN THIS PROCESS, IN WHICH THE ESSENTIAL OF THE REDUCTION DIVISION IS EFFECTED, IT IS NOT LONGITUDINAL HALVES OF CHROMOSOMES BUT ENTIRE CHROMOSOMES WHICH SEPARATE FROM ONE ANOTHER. The result of this is that each daughter nucleus receives only half as many chromosomes as were found in the tissue cells of the same plant, and that these chromosomes may be male or female. Since chromosomes of corresponding lengths are always associated in the gemini, one being derived from the male and the other from the female parent, and these chromosomes separate from one another in the reduction division, each haploid daughter nucleus must inherit some chromosomes from the father, and others from the mother. Which chromosomes come from the one or other parent appears to be determined by chance. The formation of the daughter nuclei is completed (10) as in an ordinary division, but following promptly on the first reduction division, which is also known as the HETEROTYPE division, comes a second or HOMOTYPE division, which in all essentials follows the typical course (11, 12). Thus two rapidly-succeeding nuclear divisions are characteristic of most cases of reduction. In the homotypic division longitudinal halves of chromosomes separate as in the typical division. A difference from the latter is that the chromosomes are not split longitudinally in the prophase of the homotypic division itself, but, as it seems, were already split in the prophase of the preceding reduction division without the halves thus formed separating.

The fundamental difference between the typical and somatic nuclear division and the reduction division may be made clearer by means of a diagram. Fig. 234 *A* represents a somatic division with longitudinal splitting of the chromosomes. In *A a* six longitudinally split chromosomes, distinguished by the different shading, are shown arranged to form the nuclear plate. The two middle ones are seen from the end, the others from the side. In *A b* the separated halves of these chromosomes are shown on their way to the poles of the spindle in order to form the daughter nuclei. In Fig. 234 *B* the reduction division is diagrammatically represented. The six chromosomes of Fig. 91 *A* are shown in *B a* similarly

shaded and united in three gemini. The two lateral gemini are seen from the side, the middle one from the end. The latter one shows the longitudinal split in the component chromosomes and the orientation of the plane of fission. In *B b* the chromosomes of each geminus have separated and are moving towards the poles of the spindle to form the two daughter nuclei. The two halves of each chromo-

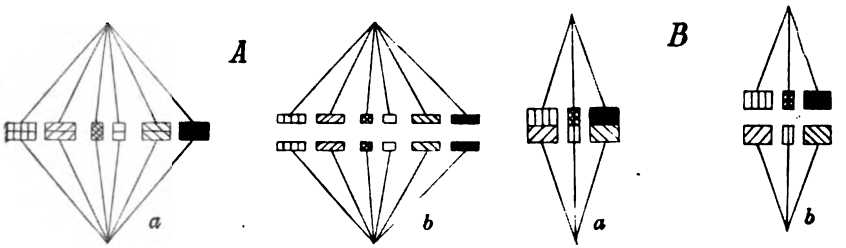


FIG. 284.—Diagrammatic representation of ordinary nuclear division (*A*) and of the reduction division (*B*). (After STRASBURGER.)

some thus go to the same daughter nucleus. This division results in a reduction of the chromosome number from six to three. In contrast to this reduction division, which, because whole chromosomes separate, results in a definite difference of the products of division, may be placed the somatic nuclear division. This, since the longitudinal halving of the chromosomes gives rise to completely equivalent products of division, may be termed equation division.

Opinions are divided as to how and when the chromosomes in the reduction division become associated in pairs, or temporarily united in a single structure. It is possible that the scheme of the reduction division is not always the same. Usually the chromosomes appear placed side by side in the pair (parasyndesis), but in some cases they appear to be placed end to end (metasyndesis).

SECTION IV

THE THEORY OF DESCENT AND THE ORIGIN OF NEW SPECIES

A. The Theory of Descent ([104]).—How the organic forms living on the earth with their morphological peculiarities have arisen is one of the most important theoretical questions in morphology. The assumption once made that the kinds of plants were independently created (theory of special creation) has become gradually abandoned in favour of a theory of evolution, especially owing to the deepening of morphological knowledge and the influence of CHARLES DARWIN. This has already been referred to in the Introduction. The theory of evolution regards the existing organisms as developed from other and frequently more simply-constructed forms which lived in earlier periods of the earth's history (cf. p. 1 ff.). This fundamental biological theory now permeates morphological investigation so completely that it is indispensable for the morphologist to be acquainted with the evidence for it. Evidence is afforded by classifica-

tion, morphology, the geographical distribution of plants and animals, and by palaeontology.

1. EVIDENCE FROM CLASSIFICATION.—According to the theory of special creation the various species of plants were created independently and are essentially constant. They were supposed to be so little subject to change that one species could not arise from another; at most a species could give rise to more or less inheritable varieties. This view thus assumes that there are sharp limits between the species, and also that there is an essential difference between species and varieties. As the student of classification proceeds to examine any group of organic forms he finds that there are no characters to be relied on to distinguish varieties from species. The amount of morphological difference between the species of a genus, the varieties of a species, or between species and varieties, is quite undetermined. It has also come to be recognised that species are not independent morphological units but in many cases are comprehensive groups of forms or *petites espèces* (*e.g.* in the genera *Erophila*, *Rubus*, *Rosa*, *Hieracium*, *Quercus*). The sharp differentiation of such species from other species, *i.e.* other groups of forms, is frequently difficult or scarcely possible. The constant small species often differ less than do many so-called varieties. It thus becomes a matter of taste or "systematic sense" whether a particular form should be regarded as a species or a variety and how a species should be delimited. The rule formerly relied upon, that crosses between two independently created species would be sterile while those between two varieties of a species would be fertile, has proved untrustworthy; fertile and sterile hybrids are known both between two varieties and two species. There are not only transitions between species but between genera and even families, so that in these cases also the limits have to be drawn at the discretion of the systematist. All these facts only become comprehensible if it is assumed that species were not independently created but are capable of heredity with variation, so that new species can be derived from others by inherited changes, while more marked changes give rise to new genera or families. On any other assumption it remains inconceivable why organisms can be placed in groups of lower and higher order (species, genera, families, classes, etc.), which are in part coordinate (like the species of a genus or the genera of a family) and in part subordinated to others (like the species to the genus or the genera to the family); further, that the groups of extinct organisms which lived in earlier geological periods can as a rule be naturally placed in the same classification as the existing forms. All these difficulties disappear when organisms are regarded as blood relations, and the natural system as expressing their nearer or more distant relationship, and thus, in a certain degree, as a genealogical tree of living beings.

2. MORPHOLOGICAL EVIDENCE.—Certain facts are inexplicable on the theory of special creation, while they are naturally explained on the theory of descent. The common morphological plan of construction exhibited by the members of a systematic group, such as a genus, a family, or a class, is of this nature. It extends in a sense to all organisms as shown in the cellular structure and the nature of protoplasm. On the other hand, the theory of evolution may explain the unexpected occurrence of certain features in a group when the plan of construction would not have led us to anticipate them (*e.g.* the spermatozoids in the pollen-tube of the Cycadeae). The great groups of the Bryophyta, Pteridophyta, and Gymnosperms, with all their morphological differences, are essentially similar in the course of development and alternation of generations, and in the construction of their sexual organs. Only on the assumption of a blood relationship can one understand how organs of different species, that appear completely different and perform different functions, prove on morphological investigation to be homologous, or that the organs of one and the same organism are so frequently homologous in spite of their diverse structure and functions. For example, thorns and tendrils are "transformed" leaves, stipules, stems, or roots; the cotyledons, scale-leaves, bracts, sepals, petals, stamens, and carpels of a plant are all "transformed" foliage leaves. All these metamorphoses of organs have evidently taken place during the phylogenetic development. In the same way reduced functionless organs found in some plants have been derived from plants in which the corresponding organs are still well formed. In the family of the Scrophulariaceae (Fig. 235) the number of stamens ranges from five in *Verbascum* to two in such forms as *Calceolaria*; in the genus *Scrophularia* one stamen of the five is present in a reduced condition, while this stamen is wanting in *Digitalis*; in *Gratiola* two fertile and two reduced stamens are present, in *Veronica* two fertile stamens only, and in *Calceolaria* only two half-stamens. Useless reduced organs are difficult to understand on the theory of special creation. Occasionally an unfamiliar character appears in a plant which can only be regarded as a reversion to a long-lost feature of its ancestors; examples are afforded by the occasional fertility of

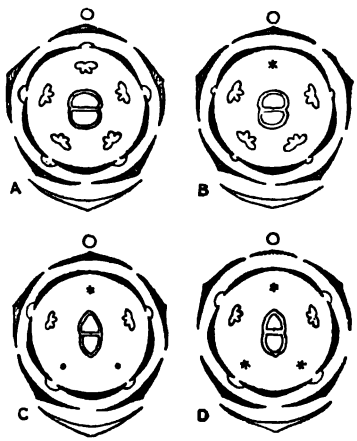


FIG. 235.—Floral diagrams of Scrophulariaceae. *A*, *Verbascum nigrum*; *B*, *Digitalis purpurea*; *C*, *Gratiola officinalis*; *D*, *Veronica Chamaedrys*. The sterile stamens are represented by black dots, and the position of completely aborted stamens by crosses. (*D* after EICHLER.)

reduced stamens or the appearance of reduced or fertile stamens in positions where fertile stamens were present in the ancestry. The similarity of the embryos of very different organisms, which is most strikingly shown in the animal kingdom, is a further indication of genetic relationship. So also is the fact that occasionally the embryos are more highly organised than the mature organism (in some reduced organisms, *e.g.* many parasites). The juvenile leaves on the seedlings of some plants which are adapted to extreme conditions of life may resemble the ordinary leaves of less specialised species of the same genus (*e.g.* in *Acacia*, Fig. 136). Not infrequently a species repeats more or less completely in its ontogenetic development what we assume on other grounds to have been the course of its phylogenetic development (BIOGENETIC LAW).

3. EVIDENCE FROM GEOGRAPHICAL DISTRIBUTION.—Geographical limits which hinder free migration (*e.g.* high mountains, and seas in the case of land plants and masses of land in the case of marine organisms) stand in striking correspondence with differences in the fauna and flora of particular habitats, countries, continents, or oceans. The assemblages of organisms found in two continents differ as regards their families, genera, etc., in proportion to the degree of present and former isolation because the forms in each region have continued their phylogenetic development independently. The easier the exchange of forms between two regions the more numerous will be those which are common to both. It is a general rule that the inhabitants of any region are most closely related to those of the nearest region from which migration may be assumed, on geological and geographical reasons, to have taken place. This holds, for example, for the Cape Verde Islands and the African mainland, and for the Galapagos islands or Juan Fernandez and the neighbouring regions of America. The more a habitat, such as an island, is isolated from the rest of the world the richer will it tend to be in peculiar forms (ENDEMISM); these often differ only slightly from other non-endemic forms from which they have evidently originated, though further dispersal has been impossible.

4. PALAEONTOLOGICAL EVIDENCE.—Palaeontology shows that in the history of the earth species have become extinct and others appeared; that not infrequently the forms in successive geological strata can be arranged in series showing progressive organisation; and that the groups which are regarded as most highly organised appeared relatively late in the history of the earth (*e.g.* the Angiosperms in the Cretaceous period). It has also made us acquainted with extinct intermediate types between genera, families, and classes. That such cases are not more frequent evidently depends on the incompleteness of the geological record. In Botany the most important of these synthetic groups is that of the Pteridospermeae or Cycadofilices, which are plants of the Carboniferous period connecting the Ferns

and the Cycadeae; they have leaves like the former but seeds like the latter, while anatomically they present resemblances to both.

5. DIRECT EVIDENCE OF THE VARIABILITY OF SPECIES.—All the preceding sources of evidence gain in significance from the direct observation of the inconstancy of some species. Careful observation establishes the appearance, both under natural conditions and, more frequently, in cultivation, of inheritable deviations which would have the systematic rank of varieties or species. It has also been possible in various ways to experimentally produce new forms the characters of which are inherited. The importance of such observations is that they give some insight into the problem of the formation of species and the origin of new morphological characters.

B. Formation of Species and the Origin of Adaptations.—All observations have so far shown that the inheritable changes in organisms may concern this or that character, may be larger or smaller, and are irregular in origin. This serves to elucidate the great variety in organic forms. These abrupt changes may be harmful, indifferent, or useful to the organism. If they are so injurious that the life of the organism is scarcely possible, the variety will disappear as quickly as it originates (*e.g.* seedlings that have lost the power of forming chlorophyll). To what extent such inheritable changes arise under the influence of external conditions has yet to be determined in particular cases; it will be treated of in the physiological portion of this text-book.

Since the acceptance of a theory of evolution it has been evident that the origin of the ADAPTIVE CHARACTERS of organisms called for special explanation. The recognition that living beings vary in all directions does not afford insight into the striking fact that organisms are in many ways adapted to their environment, and organs more or less adapted to their functions, while the reactions of the organisms are beneficial. This condition of adaptation or inherited adaptedness must in some way have originated phylogenetically. As to how it arose, observations and experiments have to the present given no direct answer. Explanations have been sought in a different way, the two most important hypotheses being known as Lamarckism and Darwinism.

1. **Lamarckism** ([105]).—This hypothesis starts from the fact that some organisms assume a different form according to the surroundings in which their germ cells develop to the mature organism, without losing the power of developing differently in another environment. Thus there are plants which can live both on land and in the water (amphibious), assuming different forms according to the environment. When grown on land they have the form and internal structure of typical land plants; when cultivated in water they resemble typical aquatic plants. Some plants under dry conditions of cultivation produce xerophilous characters, while when grown in moist air they

are hygrophilous. This power of reacting to different environments by the development of different characters is known as the capacity of modification. Such MODIFICATIONS (cf. Physiology, p. 322) are not inheritable in the sense that the seeds of, for example, an amphibious plant which has developed in water to a water plant will produce the aquatic form if they are sown on land. On the contrary, the land form is always produced on land and the aquatic form in water whether the seeds have been taken from the one form or the other.

These influences of the environment have been regarded as direct adaptations on the part of the plant which has the power of thus modifying itself. The power has further been attributed to the organism of responding by a useful reaction to every external influence, even to those not met with under natural conditions. Such a power of adaptation would apply to new functions as well as to external factors; the need of an organ would bring about its formation. It is further assumed by Lamarckism that every modification, especially those resulting from external factors or the needs of the organism, is inheritable, or at least can become inheritable in the course of time. Thus when a plant has been for generations directly adapted to aquatic life, to life in the shade, or at the expense of another organism, the acquired peculiarities of structure gradually become fixed, *i.e.* they also appear when the occasion for them is no longer present. Regarding this view it must first be remarked that the assumption "a need for an organ can bring about its formation" is not clear, and also that nothing is known of the inheritability of those effects of external conditions that have been termed modifications above. For these reasons alone Lamarckism must be given up. Further, it is difficult to conceive that the organism should react usefully in anticipation of particular external factors. As a matter of fact we not uncommonly meet with reactions to new unaccustomed stimuli which appear quite indifferent or even harmful. Thus the tentacles of *Drosera* become curved at a high temperature just as if they were in contact with an insect. Leaves cut off from a plant may continue to live for years by producing roots even when they are unable to form shoots. When there appears to be direct adaptation to various stimuli (*e.g.* water, light, air, shade, etc.), to which particular organisms are exposed in their habitats, the result may be otherwise explained. It may be assumed that such organisms already possess the capacity or the factors which enable them to follow this or that course of development according to the external conditions. The external conditions would not produce the factors but only determine their becoming manifest or not. How these factors have historically come about, and why some organisms possess them and others not, why, for example, only some plants are adapted to live in water as aquatic plants or as land plants on the land, remains still unexplained. On this question Lamarckism throws no light.

2. Darwinism ([104. 106]).—DARWIN starts from the fact that the limited conditions for life on the earth do not permit of unlimited increase in the number of organisms. Nearly every living being produces during its individual existence so many germs that were all to grow the whole earth would in a short time be overpopulated. That so few descendants of an individual survive is due to many being destroyed at all stages from the germ cell onwards. They are overcome in the STRUGGLE FOR EXISTENCE with the environment, in which other organisms of the same or different species are included. Were all the offspring alike, accident only would decide which should survive, and such accidents do play a great part. Since, however, inheritable differences occur among the offspring, those individuals will as a rule be favoured in the struggle for existence which by their peculiarities are capable of maintaining themselves, or are more capable than the others in the particular situation to which chance has brought them. Thus a process of selection (NATURAL SELECTION) comes about. If, further, the selected variants hand on their properties to their descendants, and the variation and the struggle for existence is repeated, the process must lead to the selection of still better adapted forms. Organisms may arise with any sort of characters, useful, indifferent, or harmful. Since, however, those with injurious qualities promptly disappear, those that remain are better adapted than those that perish. Usefulness which was not explained by Lamarckism (where the useful capacity of reaction in relation to new conditions of the environment was assumed) comes about according to Darwinism from the preservation of new inheritable properties which contribute to the success of the organism in the struggle for existence. It is in this that the great advance made by DARWIN'S theory, as compared with Lamarckism, consists. It is supported, as has been seen, by the observations hitherto made on the origin of new inheritable characters in organisms, although the assumptions of Darwinism leave various difficulties to be overcome.

DIVISION II

PHYSIOLOGY

DIVISION II

PHYSIOLOGY (1)

THE object of Physiology is to describe the phenomena of life, to study their dependence on external factors, and so far as possible to trace them back to their CAUSES. Physiology, like Chemistry and Physics, is concerned with inquiries into the causes of what takes place. It must, however, also take into consideration the significance to the organism of what happens. In its methods as well as in its problems Physiology agrees with Physics and Chemistry; its methods are EXPERIMENTAL.

The main results of physiological investigation are the following:

1. There is no fundamental distinction between the vital phenomena of animals and plants. This is not surprising, since plants and animals are only morphologically distinct in their more advanced representatives. In the physiological sphere it becomes more and more clear, as investigation proceeds, how similar the course of life in the two kingdoms is. The physiology of organisms is thus really a single subject. A text-book of botany has evidently only to give an account of the physiology of plants, but, where this is useful, analogous phenomena in the animal kingdom will be mentioned.

2. In some respects the behaviour of the living plant does not differ from that of non-living bodies. In spite of the large amount of water which it contains, the plant is as a rule solid, and has the physical properties of such a body. Weight, rigidity, elasticity, conductivity for light, heat, and electricity are properties of the organism as they are of lifeless bodies. However important these properties may be to the existence and the life of the plant, they do not constitute life itself.

3. The ESSENTIAL PHENOMENA OF LIFE are strikingly different from the processes met with in non-living bodies. They are intimately connected with the protoplasm and depend on the peculiar fashion in which this substance reacts to influences of the outer world, *i.e.* upon its IRRITABILITY and CAPACITY OF REGULATION.

(a) Irritability.—In the reactions of the organism the connection between the causal influence and the effect induced by it is not so apparent as it is in chemical or physical processes. This

depends on the part always taken by the protoplasm, so that the reaction observed is not the direct effect of an external cause, but a very indirect result. Further, according to the condition of the protoplasm, the same factor may produce different effects. An example will make this clear.

If the free end of a flexible rod is placed horizontally, it will bend downwards to a definite point as the result of its weight. A part of a plant will behave similarly, and if dead, as for instance a withered stem, will remain in the position it thus assumes. If, however, a living growing stem has been used in the experiment it will exhibit an effect of gravity which is very surprising in comparison with the purely physical effect. The growing portion of the stem curves, and by its own activity becomes erect again; it thus moves against the force of gravity. If the experiment is made with a tap-root, this will curve vertically downwards much further than its own weight would cause it to do. A rhizome (*e.g.* of *Scirpus*), on the other hand, will place its growing tip horizontally when it has sunk by its own weight out of the horizontal plane. In these three experiments the physical conditions are the same. The weight of the earth acts on a horizontally-placed portion of a plant. The results in the three cases are as different as possible.

The explanation of this remarkable behaviour of the plant is to be sought in the fact that, while to begin with gravity influences it as it would influence an inorganic structure—giving weight to the mass—this primary physical change then acts as what is called a stimulus. This liberates inner activities of the plant which have neither quantitatively nor qualitatively a recognisable connection with the force of gravity. Such relations become clearer if the organism is compared with a mechanism. The connection between the light pressure of the finger on the trigger of a gun and the flight of the bullet is not a simple one. The pressure first liberates a trigger; the energy thus obtained drives the hammer on to the percussion-cap; this explodes and causes the powder to explode; the gases liberated by the explosion force the projectile from the barrel. It is clear that the force of the hammer bears no relation to that of the pressure of the finger of the marksman, and there is just as little connection between the amount of force generated by the expansion of the powder and that exerted by the hammer of the gun. There are energies present, those of the trigger and powder, which are set free. Such liberations of energy, especially when they follow in order and constitute a chain of processes, are of very frequent occurrence in the organism. They are known as phenomena of irritability, and the factor which starts them is termed the stimulus. They are always found when the specific phenomena of life are concerned.

Just as the action of a machine is only comprehensible when its construction is known, a knowledge of the external form and internal structure of the plant is a necessary preliminary to its physiological study. It has been seen, however, that it is not possible to understand the function from the structure to the same degree in the case

of the plant as it is in that of a machine. In the organism we are concerned not with the mechanical interaction of parts but with a succession of chemical reactions. While it is true that the phenomena of life cannot as yet be thoroughly explained, this does not negative the conviction that they only differ from the processes in inorganic bodies by their much greater complexity; in principle a physico-chemical explanation of vital phenomena can be attained.

(b) Capacity of Regulation.—The study of machines not only assists in the comprehension of a liberating stimulus but further renders clear the second widely-spread property of organisms, *i.e.* their regulative power. As in a machine the speed may be automatically maintained at a particular level, so in numerous processes in a plant there is an element which controls the result both as regards quality and quantity. Though self-regulated processes are not wanting in the inorganic world, they do not occur abundantly as they do in the organism. ON THIS ACCOUNT THE POWER OF REGULATION MAY BE REGARDED, TOGETHER WITH THE IRRITABILITY, AS A SPECIALLY IMPORTANT CHARACTERISTIC OF LIVING BEINGS.

4. So long as the organism is actively living, an unbroken chain of changes can be recognised in it which are exhibited in the three following ways:

(i.) An organism, which appears to us as an individual, does not consist of the same unchanged material, even when no further growth in size is taking place. While its external form remains constant, progressive changes go on internally. New substances are taken up from without, are transformed within the plant, and are again given off from it. The organism has a METABOLISM. Inorganic nature offers us no process analogous to this.

(ii.) As a rule, however, metabolism does not proceed so that the absorption and giving-off of material are equal, but more is absorbed than is given off. The mass of the organism is increased, it GROWS. Growth is also known in the cases of chemical precipitates or deposits, and of crystals. In these cases it tends to proceed in such a way that no essential change of shape takes place (crystals), or that the changes in shape are accidental and irregular (precipitates). The organism, on the other hand, by changes of its form assumes quite definite shapes, which follow in regular order. It passes through a DEVELOPMENT which leads sooner or later to the production of new organisms or daughter individuals; REPRODUCTION takes place. Growth, development, and reproduction are processes highly characteristic of living beings.

Some precipitates have a certain external similarity to plants under certain conditions. If some sulphate of copper to which sugar has been added is introduced into a solution of ferrocyanide of potassium and common salt containing gelatine, a precipitate of ferrocyanide of copper is formed. This to all appearance grows, and in its form recalls that of plants. This "artificial plant" lacks, however,

not only the internal structure of a true plant, but especially the power of reproduction and of regular development.

(iii.) Lastly, organisms exhibit powers of MOVEMENT; they either change their positions bodily, or they bring larger or smaller parts of their bodies into other positions. Since inorganic bodies and dead organisms may exhibit movements, it is only the kind of movement and the means by which it is brought about that are characteristic of living beings.

In nature the three processes mentioned above, metabolism, development, and movement, usually go on simultaneously. Metabolism without movement of the substances concerned is impossible; development is bound up with metabolic changes and with movements; and, lastly, movements cannot occur without metabolism. Nevertheless, we may for descriptive purposes consider the three processes separately, and thus divide Physiology into the following sections:

(1) The study of metabolism or chemical physiology, which may also be termed the physiology of nutrition.

(2) The study of development or the physiology of form, changes of shape, and the mechanism of development.

(3) The study of movement.

5. The full vital activity of the plant is only attained when a number of conditions, which may be divided into internal and external, are fulfilled (2). The internal causes of life are connected with the protoplasm. Its structure and organisation not only determine that the changes which take place in the organism have a vital character, but that the organism shows specific differences depending on the descent of its protoplasm. Thus the most fundamental condition of life is the presence of a living mass of protoplasm. All other conditions of life can be created or removed at will. The protoplasm, on the other hand, cannot be artificially synthesised, and only arises in the organism by the activity of existing protoplasm.

The protoplasm can, however, only carry on its activity by continual interaction with the surrounding world. The influence of the latter is threefold. It provides the material from which the body of the plant is built up; it acts as the source of liberating stimuli (p. 216); it provides the plant with the necessary energy either in the chemical energy of substances absorbed from without or as vibrations of the ether.

In the external factors that are of importance for the life of a plant, a distinction must be drawn between the necessary and the inessential factors. Indispensable conditions of vital activity are a certain temperature and the presence of certain substances, as well as the absence of others that act injuriously or fatally (poisons). On the other hand, light is not in such a general sense a necessary condition for life. Some plants require direct sunlight, at least for their aerial organs, while others avoid this and seek the shade (shade

plants); others can pass through their whole life-history in complete darkness.

The necessary factors must further be present within certain definite limits. An excess (above the maximum) or too little (below the minimum) is alike injurious, and at a certain intensity (optimum) the best results are obtained. MINIMUM, OPTIMUM, and MAXIMUM are recognisable in the dependence of every vital phenomenon on an external factor, and are called the CARDINAL POINTS of the influence of this factor. They are by no means constants; they differ for particular organisms and particular vital phenomena; they change with the duration of the influence of the factor, and they depend on the condition of the plant, and on other external factors.

Every transgression of the minimum, or the maximum, for an external factor leads sooner or later to death. This may result from too high a temperature or from too low a temperature, from too much or too little light, or from an excess or an insufficiency of some substance. Thus when too little water is given a plant dries up, or when a substance is present in excessive and injurious amount a plant may be poisoned.

Most plants are killed by being frozen (3) at sufficiently low temperatures. Nearly all are killed by high temperatures that are far below the boiling point of water. Only some Cyanophyceae can endure the very high temperature of certain hot springs.

Susceptible plants, especially those of a tropical climate, are killed even at temperatures above 0° C. Others are killed by the formation of ice in the tissues, while some may be frozen hard in winter without suffering any harm. *Cochlearia fenestrata* in Northern Siberia endures a temperature of −46° C. without injury, and some forest trees can stand even −60° C. The resistance of lower organisms to extreme cold is noteworthy. Thus in PICTET's experiments Diatoms endured for a long time a temperature of −200° C.

By increase of the intensity of light any cell can be killed; in different cases the action of the light may be either mainly chemical or mainly thermal. Many Bacteria are killed even by bright daylight; on this depends the important hygienic effect of light in houses and dwelling-rooms.

The need of light not only changes from one species of plant to another, or from individual to individual, but the optimum effect of light may change for the same individual as it develops. Many of the cultivated plants of the tropics, *e.g.* Coffee and Cocoa, require shade when young, and need to be at first protected by shade-giving trees (species of *Albizzia, Musa*) planted for this purpose. When older they bear or even require exposure to the full tropical sun.

Among the influences of particular substances that of WATER is especially evident. When light and temperature are at the optimum, as is the case in the tropics, the development of plants depends above all on the supply of water. In regions with a large rainfall, uniformly distributed throughout the year, a most luxuriant vegetable growth occurs as in the formation of the TROPICAL RAIN FOREST. A regularly recurrent dry period determines DECIDUOUS FOREST, a lesser rainfall permits of the formation of SAVANNAHS, and still more reduced precipitation leads finally to a DESERT (4).

Few plants can bear prolonged drying and the associated loss of water. Often

death at low temperatures results, not from the direct influence of the cold, but from the insufficient absorption of water, the roots being unable to take from the cold or frozen soil enough water to make good the transpiration from the sub-aerial organs.

6. Death does not necessarily at once result when the minimum or maximum for external factors is overstepped. The organism has frequently passed into a condition of LATENT LIFE, and this may also come about from internal causes. It is often difficult to decide from inspection whether an organism is in the condition of ACTIVE LIFE, of LATENT LIFE, or of DEATH. Latent life has this in common with death, that all vital activities are arrested; but while active life can be resumed from latent life, this is impossible when the organism is dead.

Many resting stages of plants, such as seeds and spores, pass into the state of latent life. They are then as a rule far more resistant to desiccation, heat, and cold than organs in an active condition. Thus spores of Bacteria can bear a moist heat of 100° C. and more, and the same holds for some seeds, such as those of species of *Medicago*. On the other hand, spores and seeds in the dry condition resist a low temperature even of −253° C. (5)

SECTION I

METABOLISM (6)

I. The Chemical Composition of the Plant (7)

Any consideration of the metabolic changes in the plant requires a knowledge of its chemical composition. This is studied by chemical methods.

Water and Dry Substance.—Some insight into the composition of the plant can be obtained without special means of investigation. Every one who has dried plants for a herbarium knows that the plant consists of water and dry substance. He also knows how the removal of the water influences such fundamental physical properties of the plant as its rigidity and elasticity. By means of weighing it is easy to show how large is the proportion of water in the total weight of the plant. For this purpose it is not sufficient to expose the plant to the air, for when air-dried it still retains a considerable proportion of water, which must be removed by drying in a desiccator or at a temperature of over 100° C. It can thus be ascertained that the proportion of water is very considerable; in woody parts some 50 per cent, in juicy herbs 70-80 per cent, in succulent plants and fruits 85-95 per cent, and in aquatic plants, especially Algae, 95-98 per cent, of the weight of the plant consists of water.

Ash.—While we can thus distinguish by drying between the water and the dry substance of the plant, we are able by burning to distinguish between the combustible or organic material and the incombustible substance or ash. The fact that the plant leaves an ash is evident in the burning of wood or in the smoking of a cigar; the microscope further shows that even minute fragments of cell wall or starch grains leave an ash on burning. Information as to the quantitative relations of the ash is afforded by analysis, which shows especially that the various organs of a plant differ in this respect; leaves, for example, tend to contain more than stems. It has thus been found that the dry substance of the leaves of *Brassica rapa* contains about 20 per cent of ash, while the stems have only 10 per cent (cf. p. 238).

The constituents of the ash also vary according to the nature of the soil and other external influences. On the other hand, distinct species may accumulate different quantities of mineral substances, even when exposed to the same external conditions.

While the majority of the more common elements occurring in the earth are found in the ash of plants, only a few elements are present in sufficient amount to be quantitatively estimated. These are the non-metals Cl, S, P, Si, and the metals K, Na, Ca, Mg, and Fe.

Organic Substance.—Chemical analysis is not needed to show that the plant contains carbon in a combined form. Every burning log or match shows by its charring that it contains carbon. The examination of a piece of charcoal in which the finest structure of the wood is retained, shows further how uniformly the carbon is distributed in the plant, and how largely the substance of the plant consists of this element. Accurate weighing has shown that carbon constitutes about one-half of the dry weight of the plant. On combustion of the dry plant the organic substance is changed, and passes off in the form of carbon dioxide and water, ammonia or free nitrogen. It contained the elements H, O, N, and C chemically combined; some of the elements mentioned as occurring in the ash may also occur in organic compounds.

Source of the Materials.—There are thus only the following thirteen elements found in considerable quantity in the plant:

H, Cl, O, S, N, P, C, Si and Na, K, Mg, Ca, Fe.

When the plant is growing their amount is continually increasing in the plant, and they must therefore be continually absorbed from without.

As a rule, only gases and liquids can enter the plant; solid substances have to be brought into solution before they can pass through the firm cell walls. When, however, cell walls are absent, as in the Flagellates and Myxomycetes, the naked protoplasm is able to surround and thus to absorb solid particles.

The chemical composition of animals is essentially similar to that of plants. The absorption of food in animals takes place by means of the digestive system. The contrast is, however, not so great as appears at first sight, for as a rule the food materials are converted into a fluid condition before they are absorbed by the cells.

II. The Nutrient Substances: their Absorption and their Movement within the Plant

The materials taken into a plant may be necessary, unnecessary, or harmful. In any particular case this can only be decided experimentally, for it would lead to erroneous conclusions to assume that all substances constantly present in a plant are necessary. It has indeed been found that only ten of the thirteen elements mentioned above are indispensable. They enter the plant not as elements but as compounds. We can distinguish as the three main groups of nutrient substances—(*a*) water, (*b*) salts dissolved in water, (*c*) gases.

A plant cannot exist without a continual supply of nutrient substances. This is evident in the case of a growing plant in which the increase in size of the body is at the cost of the material absorbed from without. The fully-grown portions of the plant also require a steady supply of new material, since their metabolism involves a constant loss of substance.

(a) Water

All the chemical changes which take place in the metabolism of the plant are carried out in WATERY SOLUTIONS. For this reason WATER IS AN INDISPENSABLE CONSTITUENT of the plant. All portions of the plant are permeated with water, and the protoplasm, the basis of life, always contains 75 per cent or upwards of water. The plant can only carry on its life fully when in this condition of saturation with water. Any considerable diminution in the amount of water either destroys the life permanently, or at least so greatly diminishes the manifestations of life that they can no longer be observed.

With the exception of some succulent plants which are uninjured by the loss of nine-tenths of their water, plants as a rule have their activity impaired by the loss of water in withering, and are killed by complete desiccation. It is always to be regarded as due to some special provision or exceptional quality when entire plants, or their reproductive bodies which have been dried, can be again brought to life by a supply of water. Thus, for example, some epiphytic Ferns, some Algerian species of *Isoetes*, and the Central American *Selaginella lepidophylla*, can withstand droughts of many months' duration, and on the first rain again burst into life and renew their growth. In like manner many Mosses, Liverworts, Lichens, and Algae growing on bare rocks, tree-trunks, etc., seem able to sustain long seasons of drought without injury.

Seeds and spores after separation from the parent plant can as a rule endure

drying and remain productive for a long time. In this case also all vital manifestations cease in the dry condition.

Many seeds lose their power of germination after having been kept dry for only one or a few years; others even after a few days; and others again cannot endure drying at all. It must not be forgotten that in all these instances a certain amount (about 9-14 per cent) of hygroscopic water is retained by plants even when the air is quite dry. Over the sulphuric acid of the desiccator seeds retain for weeks 6 per cent or more of their weight of water. Even drying at 110°, or the action of absolute alcohol, can be borne by some spores and seeds.

Absorption of Water

Absorption of Water by the Cell.—All parts of a plant and all the parts of its individual cells are saturated with water. The cell membrane has the water so freely divided between its minute particles that the water and the solid substance are not distinguishable under the highest magnification. If the water is allowed to evaporate, air-filled cavities do not appear in its place, but a contraction of the cell wall takes place. On the other hand, the absorption of water by dry or not fully saturated cell walls causes a swelling of the latter. The increase in volume which a body undergoes as the result of the introduction of fluid is termed IMBIBITION (δ); the amount taken up is limited for a particular temperature. There are substances which swell in alcohol or xylol; the vegetable cell wall, however, swells in water. The walls of lignified cells absorb about one-third of their weight of water, while those of many Algae and some seed-coats and pericarps absorb several times their weight. This takes place with considerable energy, and can therefore overcome considerable resistance.

The air-dry protoplasm of many seeds and spores imbibes water and swells just as does the cell wall. Like gum arabic, however, it loses the characters of a solid body and passes into a colloidal solution. This is the condition of the protoplasm, as a rule, in the actively living cell, though certain portions may have a firmer consistence. Colloidal solutions have, indeed, always the tendency to pass from the fluid (sol) condition to the gel condition.

The cell sap is always a molecular solution of crystalloids in water, but may also contain colloids.

Only a cell which is not completely saturated for water can withdraw water from its surroundings. It is thus necessary to be clear as to what is meant by a cell being saturated for water. For the cell wall the answer is simple; the wall is saturated when the maximum of swelling has been reached. It is much more difficult to determine the limits of water capacity for the protoplasm and cell sap. Taking the latter first, it may be assumed for the sake of simplicity that it is a solution of crystalloids, and that it is enclosed by the cell wall only without an intervening layer of protoplasm. If a tube

of cellulose is filled with a solution, for instance of common salt, and placed in water, a process of DIFFUSION will commence. Water passes into the tube while salt passes out from it. Although the wall of the cell offers greater resistance to the passage of the salt than of the water, the diffusion if continued long enough will result in the same concentration being attained at all points both within and without the cell. A partition which is permeable to both water and salts thus only affects the process of diffusion by diminishing its rapidity. When the wall consists of a substance which is readily permeable to water but quite impermeable to the salt, the course of diffusion is essentially different. If such a SEMI-PERMEABLE MEMBRANE is employed, there is no question of a diffusion of the salt, but the conditions permit of a diffusion of water inwards. Since within the semi-permeable membrane a portion of the space is occupied by the molecules of salt, the water is here less concentrated than outside. A diffusion from the more concentrated to the less concentrated water, therefore, takes place. Such a one-sided diffusion is termed OSMOSIS (9), and it results in a condition of pressure (OSMOTIC PRESSURE) within the cell.

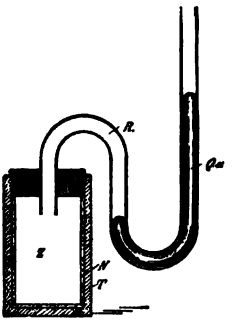


FIG. 236.—Osmometer. *T*, Clay cell with the precipitation membrane (*N*); *R*, manometer with mercury (*Q*); *Z*, sugar solution.

A physical apparatus may, in the first instance, be employed to demonstrate and measure the osmotic pressure. Since semi-permeable membranes are mostly delicate, they are supported by a solid but porous substratum; they may be deposited on the walls of cells of unglazed clay. Such a cell (Fig. 236) may, for instance, have a semi-permeable membrane of ferrocyanide of copper deposited on its inside. The cell is then filled with a solution of sugar, closed, provided with a mercury manometer, and immersed in water. The osmotic pressure is indicated by the rise in height of the mercury. It has been found that a 1 per cent solution of cane sugar can give rise to a pressure of $\frac{2}{3}$ atmosphere. Assuming that the semi-permeable membrane is impermeable to the dissolved substance, the effect of all solutions of crystalloids is nearly proportional to the number of molecules and ions present. Solutions that produce the same osmotic pressure are termed isosmotic; thus, for example, 0·58 per cent NaCl, 2·7 per cent grape sugar, and 5·13 per cent cane sugar, are isosmotic with 1 per cent potassium nitrate.

The clay cell corresponds to the cell wall and the ferrocyanide of copper membrane to the protoplasm. In the vegetable cell itself the cell wall is completely permeable apart from some special cases (9a). The layer of protoplasm applied to it, on the other hand, is more or

less semi-permeable, at least so long as it is living. As a result of this there is a one-sided passage of water into the vacuole without any corresponding passage outwards of salts. A further result is the pressure of the cell contents on the protoplasmic sac and through it on the cell wall. The protoplasm becomes stretched under this pressure (turgescence, osmotic pressure) without much resistance, but the cell wall, by virtue of its elasticity, exerts a considerable counter-pressure. This puts a limit on the absorption of water by the cell. It ceases when the amounts of water entering and forced through the distended membrane in a unit of time are equal.

FIG. 237.—Internodal cell of *Nitella*. *F*, Fresh and turgescent; *p*, with turgor reduced, flaccid, shorter and narrower, the protoplasm separated from the cell walls in folds; *ss*, lateral segments. (× circa 6. After NOLL.)

It is not necessary to go further into the question of the water-content of protoplasm. It is also necessarily limited, since the protoplasm is under pressure on the one side from the cell sap, and on the other from the cell wall.

The distension of the cell wall is often considerable and depends on the amount of the internal pressure and the elastic properties of the cell wall. In many cases the cell wall is stretched by the pressure some 10 per cent to 20 per cent, in extreme cases even 50 per cent, and it contracts when the pressure ceases. When the cell is pricked or the protoplasm killed, the pressure is removed and the wall contracts (Fig. 237). By the distension the cell wall becomes more rigid, just as a thin india-rubber balloon when air is forced into it resists changes of shape. The increase of rigidity of the plant, by reason of the turgor pressure or turgescence, is very important; it is the simplest, and in many cases the only way, in which the cell becomes rigid. This is dependent naturally upon the presence of a sufficient supply of water; if a distended cell is taken from the water and allowed to give up water in the air, the stretching of the wall disappears, and with this the rigidity; the cell wilts. With a fresh supply of water the turgescent condition can be restored. So long as a cell does not possess its maximum water-content it acts as a suction-pump, the degree of suction depending on the deficiency in water. Under such circumstances it will be evident that cells with highly-concentrated cell sap will develop the greatest power of suction.

Many chemists regard every molecular watery solution as having a definite osmotic pressure, whether this is actually effective towards

the outside or not. A wilted cell which has lost water has more concentrated cell sap, and in the chemist's sense the osmotic pressure has increased. On the other hand, the pressure acting on the membrane has diminished or is completely eliminated. This latter pressure, *i.e.* the externally effective osmotic pressure, may be distinguished as TURGOR PRESSURE, since it brings about the stiffness or turgescence of the plant. A statement that a cell has a certain osmotic pressure thus tells nothing as to the height of the turgor pressure; this will vary according to the water supply. Given a sufficient supply of water it is true that the whole osmotic pressure will be expressed as turgor pressure.

The phenomenon known as PLASMOLYSIS serves to determine the osmotic pressure. If a turgescent cell is placed in a salt solution which has a higher osmotic pressure than the cell sap, the pressure on

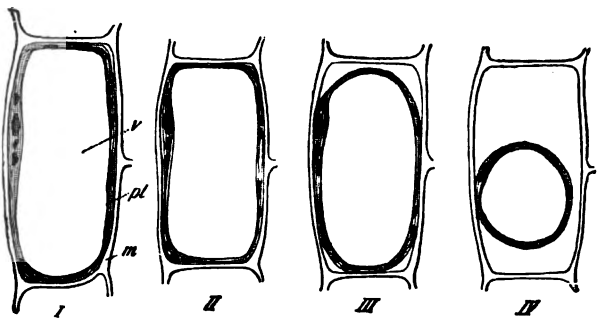


FIG. 238.—A young cell from the cortical parenchyma of the flower-stalk of *Cephalaria leucantha*. *m*, Cell wall; *pl*, protoplasm; *v*, vacuole. *I*, In water; *II*, in 4 per cent potassium nitrate solution; *III*, in 6 per cent solution; *IV*, in 10 per cent solution. (After DE VRIES.)

the membrane is removed and there is a shortening of the cell followed by a separation of the protoplasm from the wall; this begins at the angles and ultimately leads to the rounding off of the protoplast within the cavity of the cell (Fig. 238). It is immaterial what substance is employed to produce plasmolysis, but the protoplasm must be impermeable to it and not injured by it. The reason why the solution withdraws water from the cell sap is readily understood. Since the external solution contains more molecules and ions than the internal solution, the water in it is less concentrated; water therefore passes from the higher concentration to the lower until the concentration within and without is the same. If the solution employed for plasmolysis just effects the separation of the protoplasm at the angles of the cell, it can be regarded as isosmotic with the cell sap. Since the osmotic pressure of the solution is known from physical investigations, we thus arrive at the osmotic pressure in the cell. Plasmolytic determinations have shown that in ordinary cells

this amounts to 5-10 atmospheres, but can sometimes be 100 or more atmospheres. It tends to be unequal even in neighbouring cells, and may show periodic variations in connection with external conditions ([10]).

The separation of the protoplast from the cell wall does not take place so smoothly as shown in Fig. 238. The protoplasm tends to remain connected to the wall by fine strands which rupture later.

On transference to pure water the turgescent condition will be regained, if the protoplasm has not been injured by the solution. If the protoplasm is killed, however, it has become completely permeable, and the necessary condition for a one-sided pressure has disappeared. Fresh living slices of the Sugar Beet and of the Beet Root when placed in pure water do not allow the colouring matter to escape from the uninjured cells. If the protoplasm is killed, the pigment passes into the surrounding water.

High osmotic pressures are found in cambium cells (25 atmospheres), nodes of grasses (40 atmospheres), and certain desert plants (100 atmospheres). The highest pressures are met with in plants, which like those of the sea and sea-shore live in solutions of common salt, or like some Fungi succeed in sugar solutions. In these cases also the osmotic pressure of the cell always exceeds that of the surrounding solution ; it is adapted and capable of regulation in relation to the medium, and is therefore not always the same ([11]). It is easy to understand why cells with such high osmotic pressures burst when transferred to less concentrated solutions or to pure water, in which their turgor pressure is greatly increased.

The Absorption of Water by more Complex Plants.—In many lower plants all the living cells take part in the absorption of water. In more complex plants only the superficial cells are in contact with the supply of water in the environment, and absorption of water is limited to them. In the cormus, at least in the typical land plants, the absorption of water is limited to the epidermal cells of the roots. The sub-aerial parts of the plant, covered with a more or less strongly-developed cuticle, cannot under natural conditions absorb sufficient water for the needs of the plant. The root, on the other hand, is highly specialised for this purpose, both as regards its external form and the structure of its limiting layer. Since the water in ordinary soils is finely subdivided and held firmly by the particles of the soil, a large surface must be exposed by the absorbing root. This is attained by the extensive branching of the root-system and by the presence of root-hairs which become attached to the finest particles of the soil (Fig. 239).

FIG. 239.—Tip of a root-hair with adhering particles of soil. (× circa 240. After NOLL.)

The plant is connected to the soil by the numerous lateral roots and their root-hairs, and can thus obtain the water held by capillarity in the soil, as soon as by loss of water a power of suction has arisen

in the root-hairs. A plant can extract water even from a soil which appears dry. As absorption from such a soil continues the plant begins to wilt, but even in this state absorption is still taking place, though it does not go so far as to obtain the last traces of water from the soil. The process continues further in desert plants according to FITTING, since their cell sap is highly concentrated and can develop a very strong osmotic suction ([12]).

Following SACHS, BRIGGS and SHANTZ have determined the water-content of the soil at the moment of wilting. This they term the coefficient of wilting and express it as a percentage of the dry weight of the soil. They find that it has nearly the same value in different plants, but differs widely in different soils. Thus the coefficient of wilting in coarse sand is 0·9, in fine sand 2·6-3·6, in sandy loam 9·9, and in clayey loam up to 16·5.

Other Types of Absorption of Water.—Some plants do not obtain their water from the soil. They belong chiefly to two distinct ecological groups, the EPIPHYTES and the WATER PLANTS. The morphological and anatomical peculiarities found in relation to the absorption of rain and dew by the sub-aerial organs have already been dealt with on p. 184.

Movement of Water in the Plant

That a movement of water from the roots to the aerial parts of the plant must take place follows from the fact that water is required in the development of new cells in the growing regions. The plant, however, requires far more water than is needed for its construction, because it gives off large quantities of water in the form of vapour, and a less amount in the liquid form from its aerial portions. The former process is known as TRANSPIRATION, the latter as EXUDATION.

Transpiration ([13])

The vegetable cell, like every free surface of water or substance swollen with water (*e.g.* gelatine, mucilage), must give up water to the air so long as the latter is not completely saturated. Under certain conditions the loss of water from some parts of plants (*e.g.* roots, submerged portions, shade plants) is very great. Such objects exposed to dry air, especially in the sun, lose so much water that they become collapsed, limp, and wilted, and ultimately dried up. The leaves borne on ordinary land plants behave otherwise. At first sight no loss of water is perceptible from them; but they also wilt during a drought, which renders absorption of water from the soil difficult. If the supply of water to them is interrupted completely, as by cutting them off, the wilting occurs more speedily. That they as a rule do not wilt when in position on the plant evidently depends on the fact that water is supplied from below in equal amount to that evaporated from above. The giving off of water can be demonstrated by simple methods.

1. If a transpiring part of a plant is covered with a bell-jar that has been previously cooled, the water vapour given off from the plant will be deposited in the liquid form on the inside of the bell-jar, just as the aqueous vapour in our breath condenses on a cold window pane. 2. Transpiration can be very strikingly demonstrated by the change in colour of cobalt paper; filter-paper soaked in a solution of cobalt-chloride has when completely dried a blue colour which changes to red on the presence of water. If a small piece of this cobalt paper is laid on a leaf and protected from the dampness of the atmosphere by a slip of glass, the change in colour to red, that commences at once, indicates the transpiration; conclusions as to the quantity of water given off may be drawn from the greater or less rapidity of the commencement and progress of the change in colour. 3. Exact information on this point can only be obtained by weighing experiments. These show that the loss of water vapour by a plant is usually so great as to be recorded as a common balance without great difficulty in the course of a quarter of an hour. No general statement can be made as to the amount of transpiration from a unit area of transpiring surface, for this depends on many external factors, *e.g.* temperature, light, supply of water, etc., as well as on the structure of the plant.

The process of transpiration takes place in this way. An epidermal cell exposed to the air will lose some of the imbibition water of its cell wall by evaporation; this would go on until the cell wall was dried by the air if a reserve of water were not obtainable from within the cell. This is in fact obtained from the protoplasm, from which the cell wall, no longer fully saturated, withdraws imbibition water, and the protoplasm in turn makes good its loss from the vacuole. The movement of the water affects the interior of the cell, and brings about a concentration of the cell sap. Thus the conditions are established for the cell to absorb water from an adjoining cell which is not itself transpiring, and the loss of water is thus conducted from the superficial cells where evaporation is taking place into the depths of the tissue. The amount of transpiration primarily depends on the permeability to water of the cell wall. If the cell wall is an ordinary cellulose membrane the amount of transpiration will be large; when the wall is covered with wax or cuticle, or impregnated with cuticular substance, it gives off little water. Comparative investigations on suitable objects, by means of cobalt paper, show how the transpiration diminishes with the increase in thickness of the cuticular layers until it ultimately becomes practically non-existent. Corky walls behave in the same way as cuticularised layers. In their outer covering of cork, cuticle, and wax, plants possess a protection from a too rapid loss of water. A pumpkin, with its thick cuticle and outer coating of wax, even after it has been separated from its parent plant for months, suffers no great loss of water. A potato or an apple is similarly protected by a thin layer of cork from loss of water by evaporation. The green organs of plants, on the other hand, which must be able to get rid of the surplus water in order to secure the concentration of the nutrient

salts and to reduce their temperature, make little use of such protective coverings. On the contrary, it has been seen (p. 168) that they are provided, besides the adaptations to regulate the transpiration, with special contrivances for promoting evaporation. Their great surface extension may be specially mentioned.

Transpiration is not, however, limited to the cells which are directly in contact with the atmosphere; an enormous number of internal cells can get rid of water vapour when they abut on intercellular spaces. The air-filled intercellular spaces would clearly become after a short time completely saturated with water vapour were they completely closed. Communications exist, however, as we have seen, between the atmosphere and the intercellular spaces, the most important being the stomata (p. 51). The aqueous vapour can escape by these, and thus the condition of saturation of the air in the intercellular spaces is not complete. The water vapour escaping from the stomata is readily recognised by means of cobalt paper. If pieces of this are laid at the same time on the upper and lower surface of a leaf that has stomata only on the lower side, a change of colour will take place in the cobalt paper on this side, while no appreciable giving off of water will be shown for the upper side.

It is usual to distinguish stomatal and cuticular transpiration, and we may thus say that only the stomatal transpiration is of importance in the typical land plant. In plants inhabiting damp localities the cuticular transpiration becomes considerable. Though the openings of the stomata are extremely small (the breadth of the pore being 0·007 mm. and less) so that neither dust nor water can pass through them into the plant, they are usually present in such enormous numbers and so suitably distributed that their united action compensates for their minuteness. When it is taken into consideration that, as NOLL has shown, a medium-sized Cabbage leaf (*Brassica oleracea*) is provided with about eleven million, and a Sunflower leaf with about thirteen million stomata, it is possible to estimate how greatly evaporation must be promoted by diffusion through these fine sieve-like perforations of the epidermis and of the cuticular membrane which allows practically no water to pass. BROWN and ESCOMBE have shown that the movement of diffusion through this perforated membrane is as rapid as if no cuticle were present. If this is correct the question presents itself, why the plant has constructed such a complicated apparatus instead of allowing free transpiration from unprotected cells. The explanation lies in the fact that the stomata not merely facilitate transpiration, but can stop it; they serve to REGULATE the transpiration, which a cuticle cannot do. The width of the pore of the stoma can be altered by changes in the guard cells. When the pore is fully opened transpiration is maximal, and when it is completely closed transpiration sinks to zero. Since the opening and closing of the pore take place in accordance with the needs of the plant, the stomata are

organs which react in a wonderfully purposive fashion. Opening is caused by illumination and by a certain degree of humidity of the air; on the other hand, darkness or dry air effect a closing of the pore.

The movements of the guard cells are movements of irritability and are brought about by changes in turgescence. As a consequence of the peculiar thickening of the elastic cell walls of the guard cells (p. 52), an increase of the turgor pressure intensifies the curvature of the cells and a diminution of turgor lessens the curvature. The former change leads to the opening of the pore and the latter to its being closed, as will be evident from Fig. 240 without further description (cf. also Figs. 47-49).

The stomata are mainly present on the leaves, which are thus to be regarded as organs of transpiration (and of assimilation, p. 249).

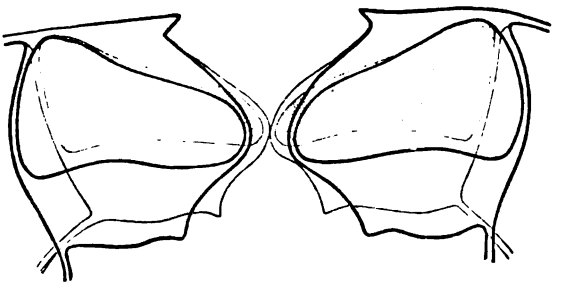


FIG. 240.—Stoma of *Helleborus sp.* in transverse section. The darker lines show the shape assumed by the guard cells when the stoma is open, the lighter lines when the stoma is closed. (After SCHWENDENER.) The cavities of the guard cells with the stoma closed are shaded, and are distinctly smaller than when the stoma is open.

The amount of water evaporated from the leaf surfaces is surprising ([14]). For instance, a strong Sunflower plant, of about the height of a man, evaporates in a warm day over a litre of water. It has been estimated that an acre of Cabbage plants will give off two million litres of water in four months, and an acre of Hops three to four millions. For a Birch tree with about 200,000 leaves and standing perfectly free, VON HÖHNEL estimated that 300-400 litres of water would be lost by evaporation on a hot dry day; on an average the amount would be 60-70 litres. A hectare of Beech wood gives off on the average about 20,000 litres daily. It has been calculated that during the period of vegetation the Beech requires 75 litres and the Pine only 7 litres for every 100 grammes of leaf substance. For every gramme of dry, solid matter produced, 250-900 grammes of water are evaporated on the average.

It is evident from these and similar experiments that more water is evaporated in a given time from some plants than from others. These variations are due to

differences in the area of the evaporating surfaces and to structural peculiarities (the number and size of the stomata, presence of a cuticle, cork, or hairy covering, etc.). But even in the same shoot transpiration is not always uniform. This is attributable to the fact that, both from internal and external causes, not only the size of the openings of the stomata varies, but also that transpiration, just as evaporation from a surface of water, is dependent upon external conditions. Heat, as well as the dryness and motion of the air, increases transpiration for purely physical reasons; while light, for physiological reasons, also promotes it. From both physical and physiological causes, transpiration is more vigorous during the day than night. Plants like *Impatiens parviflora*, which droop on warm days, become fresh again at the first approach of night. Information as to the condition of opening ([15]) of the stomata can be obtained by the use of cobalt paper (cf. p. 230) or by the method of infiltration. If the stomata are open, fluids such as petroleum, alcohol, etc., easily penetrate and inject the whole system of intercellular spaces; the leaf thus becomes translucent. If a strip of black paper is laid across a leaf the underlying stomata close. On treatment with alcohol the appearance represented in Fig. 241 is then obtained. The open condition of the stomata may also be demonstrated by the method of gaseous diffusion. If a red leaf containing anthocyan with its stomata open is placed in air containing ammonia, a blue colour develops in a few seconds; this does not take place if the stomata are closed.

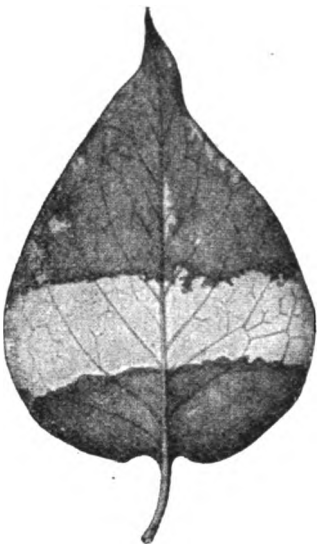


FIG. 241.—A leaf of Lilac darkened in the middle while the ends were exposed to light. Only the illuminated stomata remain open and allow the absolute alcohol to enter. (After MOLISCH.)

Plants of dry habitats which require to economise the absorbed water show numerous arrangements which protect them against excessive transpiration (cf. p. 168). In plants living in very damp situations, on the other hand, arrangements to further transpiration are found. When the leaf is able, either by absorption of heat from without or by the production of heat within itself (p. 276), to raise its temperature above that of its surroundings, transpiration is still possible even in an atmosphere saturated with aqueous vapour. In the process of exudation the plant has a further means of giving off water even after transpiration has completely stopped.

Exudation ([16])

The discharge of water in a liquid state by direct exudation is not of so frequent occurrence as its loss by transpiration, but is found

under special conditions, viz. when the plant is saturated with water and the air is saturated with water vapour. Early in the morning, after a warm, damp, but rainless night, drops of water may be observed on the tips and margins of the leaves of many of the plants of a meadow or garden. The drops gradually increase in size until they finally fall off and are again replaced by smaller drops. These are not dew-drops, although they are often mistaken for them; on the contrary, these drops of water exude from the leaves themselves. The drops disappear as the sun becomes higher and the air warmer and relatively drier, but can be induced artificially if a glass bell-jar be placed over the plant, or the evaporation in any way diminished. The excretion of drops from the leaves can be brought about by artificially forcing water into cut shoots.

The drops appear at the tips of the leaves in Grasses, on the leaf-teeth of *Alchemilla*, and from the blunt projections of the leaves in *Tropaeolum* (Fig. 242). They come from so-called WATER-STOMATA (p. 113) or through ordinary stomata, or they are secreted by small pits or hairs (sometimes by stinging hairs). All such water-excreting organs are termed HYDATHODES.

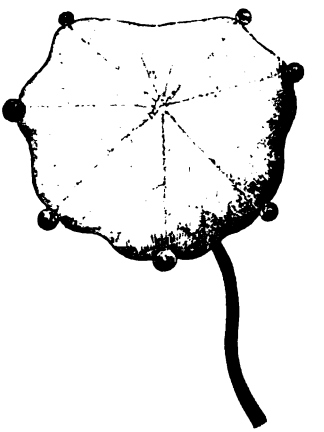


FIG. 242.—Exudation of drops of water from a leaf of *Tropaeolum majus*. (After NOLL.)

The excretion of liquid water is far more common in moist tropical forests than in temperate climates. Such exudations of water are particularly apparent on many Aroids, and drops of water may often be seen to fall, within short intervals, from the tips of the large leaves. From the leaves of *Colocasia nymphaefolia* the exuded drops of water are even discharged a short distance, and 190 drops may fall in a minute from a single leaf, while $\frac{1}{10}$ litre may be secreted in the course of a night. Again, in unicellular plants, especially some Moulds, the copious exudation of water is very evident. The water in this case is pressed directly through the cell walls, and in some cases also, as is the case in water plants, through the easily permeable cuticle.

Since the excretion of water in the liquid form can occur when the conditions are unfavourable to transpiration, especially in submerged water plants, it may in a sense take the place of transpiration in maintaining the current from the water-absorbing organs. Its physiological significance is not, however, the same as transpiration, since the expressed water always contains salts, and sometimes also organic substances in solution. In fact, the quantity of salts in water thus exuded is often so abundant that after evaporation a slight incrustation is formed on the leaves (the lime-scales on the leaves of Saxifrages and the masses of salt in some halophytes, p. 240). In some instances, also, the substances in solution in the water may play

the main physiological part in the process as in the case of the secretions of the NECTARIES, of the DIGESTIVE GLANDS of insectivorous plants (p. 258), and of the STIGMATIC FLUID.

Bleeding.—Exudation of water may often be observed after a plant has been wounded; it is regularly seen in trees and shrubs when cut in the spring, and is especially well marked in the Vine. In shrubs cut off a short distance above the ground, the extrusion of water from the wound is readily demonstrated. In this weeping or bleeding of wounds the water comes from the vessels and tracheides, and is pressed out with considerable force (ROOT PRESSURE).

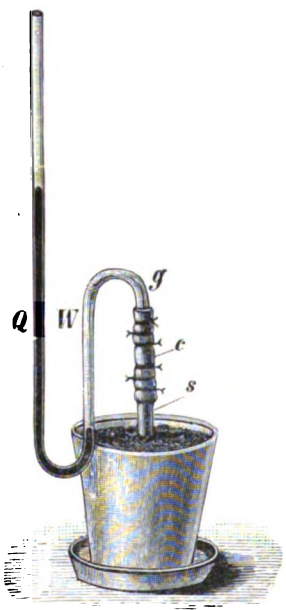


FIG. 243.—Vigorous exudation of water as the result of root-pressure from a cut stem of *Dahlia*. The smoothly-cut stem *s* is joined to the glass tube *g* by means of the rubber tubing *c*. The water *W*, absorbed by the roots from the soil, is pumped out of the vessels of the stem with a force sufficient to overcome the resistance of the column of mercury *Q*. (After NOLL.)

If a long glass tube be placed on the root-stump and tightly fastened by rubber tubing, the exuded fluid will be forced up the glass tube to a considerable height. How great the force of this pressure is may be shown by attaching to the stump a manometer (Fig. 243). The column of mercury will in some cases be forced to a height of 50 or 60, and under favourable conditions to 140 cm. or more (in the Birch). These pressures would be sufficient to raise a column of water 6, 8, and 18 metres high. The amount of water extruded is greater when the soil is kept moist and warm; it continues under such conditions, according to the kind of plant and its stage of development, some days or even months. The water may amount to many litres: up to 1 litre per day in the Vine, 5 litres in the Birch, and 10-15 litres in Palms. In parts of plants that continue bleeding for some time a certain periodicity in the amount is noticeable; more is extruded by night than by day.

The outflowing sap often contains, in addition to mineral salts, considerable quantities of organic substances (dissolved albuminous matter, asparagin, acids, and especially carbohydrates). The amount of saccharine matter in the sap of some plants is so great that sugar may be profitably derived from it. The sap of the North American sugar maple, for example, contains ½ per cent of sugar, and a single tree will yield 2-3 kilos. The sap of certain plants is also fermented and used as an intoxicating drink (birch wine, palm wine, pulque, a Mexican beverage made from the sap of *Agave*, etc.). One inflorescence of *Agave* will yield 1000 litres of sap in from four to five months.

Causes of the Excretion of Water [17].—The excretion of drops of water from intact plants is in part due to an active excretion of water from superficial cells. In other cases water is forced into the vessels, and finds a way out at the points of

least resistance (p. 114). In the phenomenon of bleeding, also, water is forced from parenchymatous cells into the cavities of the vessels; although this process takes place especially often in roots, it is not always absent in the cases of stems and leaves.

Thus, when fully analysed, all the phenomena described show a one-sided excretion of fluid from living cells. That this does not always result from the same cause is indicated by what was stated above, since the fluid is sometimes nearly pure water, at other times more or less concentrated sap.

1. The conceptions which have been formed regarding the one-sided excretion of pure water from a cell cannot readily be summarised here.

2. When the excreted fluid contains dissolved substances in considerable quantity, for example in nectaries, two possibilities present themselves. Either these substances come from within the cell and the protoplasm must have become permeable in one direction to them; or they have been formed from the outer layers of the wall and withdrawn water from the cell sap osmotically. It appears that both possibilities are realised.

Conduction of Water [18]

The water, which is partly given off in the form of vapour, especially from the leaves, and in part exudes in the liquid form from hydathodes and wounds, has, as a rule, been absorbed by the roots. It has thus to traverse a path which, even in annual plants, may amount to some metres, and in the giants of the vegetable kingdom may be more than 100 m.; the stems of *Eucalyptus amygdalina* are 100 m., those of *Sequoia gigantea* 95 m. in height. Osmotic passage from cell to cell would bring about the movement of this water far too slowly to cover the loss. The movement of water for this purpose, or, as it is called, the TRANSPIRATION STREAM, is practically confined to the woody portion of the vascular bundles, *e.g.* the wood of trees. This is shown by a classical experiment represented in Fig. 244. At Z in the branch *b* all the tissues external to the slender column of wood have been removed. Since the leaves of this branch remain as fresh as those of the branch *c*, it is evident that the transpiration current must pass through the wood and not through the cortical tissues. On the other hand, when a short length of the wood is removed from a stem without at the same time unduly destroying the continuity of the bark, the leaves above the point of removal will droop as quickly as in a twig cut off from the stem. This experiment can be performed either on intact plants or on cut-off branches placed in water; the latter for a time, until changes have taken place at the cut surface, absorb water as actively as does the intact plant by its roots. When a branch is cut off and the cut surface is placed in a solution of gelatine, which penetrates for some distance into the vessels and can then be allowed to solidify, the wood will be found to have lost its power of conducting water.

This shows that the cavities of the vessels are essential for water conduction. In the living plant, however, the vessels and tracheides always contain air in addition to water, at least when transpiration is active.

In water plants and succulents, in which little or no transpiration takes place, the xylem is correspondingly feebly developed. On the other hand, the transpiring leaf-blades have an extraordinarily rich supply of vascular bundles; these anastomose freely, so that any particular point is sure to obtain sufficient water. The illustration (Fig. 126) gives some idea of this irrigation system of a leaf-blade, but, since the finest bundles are only visible with the help of the microscope and are not represented, the system is even more complex. The conducting tracts in the stem leading to the leaves form, especially in trees which grow in thickness, a wonderfully effective conducting system. All the wood of a thickened stem does not serve this purpose; water conduction is limited to the more recently developed annual rings. When a heart-wood (p. 158) is formed this takes absolutely no part in the process.

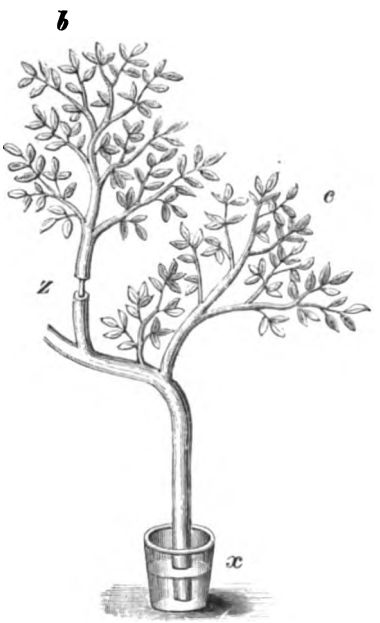


FIG. 244.—HALES' experiment to show the ascent of the sap in the wood. Although the cortex has been entirely removed at *Z*, and the wood alone left, the leaves of the branch *b* remain as fresh as those on the uninjured branch *c*; *x*, vessel containing water. Facsimile of the illustration in HALES' *Vegetable Statics*, 1727.

There is still uncertainty as to the forces which give rise to the transpiration stream. It is natural to think of a pressure acting from below, or a suction from above, and to regard the former as due to root-pressure, the latter to the process of transpiration. There are, however, a number of reasons against ascribing the movement of the water to root-pressure, and whether the suction force exerted by transpiration is sufficient to continuously raise water to the summit of a high tree appears doubtful. No generally accepted solution of the much-discussed problem of the ascent of water has yet been attained.

The following points have to be considered as regards the root-pressure. In many plants the root-pressure actually observed is very slight or absent. Even in plants with a powerful root-pressure the amount of water thus supplied in a given time is considerably less than that lost in transpiration. With somewhat more active transpiration, therefore, the root-pressure is not manifested in the way described above. When an actively transpiring plant is cut across above the

root, no water is at first forced from the stock; but, on the other hand, if water is supplied to it the cut surface absorbs it greedily (negative pressure). Only after it is fully saturated does the forcing-out of water commence. In nature root-pressure thus only comes into play when transpiration is greatly lessened, for instance at night when the air is damp and cool. The most favourable conditions for this phenomenon occur in spring when, on the one hand, the wood is richest in water, and, on the other, the transpiring foliage is not fully developed. On wounding the xylem the sap then oozes in drops out of the vessels and tracheides. A positive root-pressure in trees with foliage appears only to occur in tropical forests.

That transpiration induces a suction from cell to cell has been pointed out above, and it is clear that this suction will be continued from the parenchymatous cells into the vessels. This suction force can be readily demonstrated.

A cut shoot placed with its lower end in water shows by remaining fresh that it is able to raise the water to its uppermost twigs. This does not fully exhibit the amount of suction force which the shoot can exert, for if the latter is connected with a long tube filled with water it can support a water column of 2 metres or more in height. If the end of the tube is dipped into mercury even this heavy fluid will be lifted to a considerable height. Strong and otherwise uninjured branches of Conifers are able to raise the mercury to the height of the barometric column, and even higher, without showing signs of wilting. The connection between the end of the shoot and the glass tube must of course be air-tight. Necessary conditions for such a suction are on the one hand an air-tight closing of the water-conducting tracts such as is actually found in the plant, and on the other hand a considerable cohesive power of the fluid to be raised, which is also found to exist in practice. The conception is thus reached of a pull exerted by transpiration being conducted, owing to the cohesion of the water, to the tips of the roots of a plant. Very considerable traction forces have been demonstrated in the conducting tracts of transpiring plants as is assumed by the COHESION THEORY ([19]). This theory is, however, not yet proved. To transmit the suction downwards, the vessels would require to be continuously filled with water, while, in practice, columns formed alternately of air and water are found. When a pull took place the air bubbles would expand, and in practice air under diminished pressure is found in the vessels of actively-transpiring branches. When such vessels are cut across under mercury, this is forced for a considerable distance into the cut vessels by the force of atmospheric pressure. The supporters of the cohesion theory therefore assume that other tracts completely filled with water are present, and that those containing air merely serve as a magazine of water. It is not out of the question that the living elements always present in the neighbourhood of the vessels and tracheides may play a part in the raising of the water.

(b) The Nutrient Salts

The nutrient salts which are absorbed by a plant are almost all met with in the ash; only the compounds of nitrogen are wanting Thus the following table of the nature of the ash of a number of cultivated plants affords some insight into the amount and the distribution of the nutrient salts.

It is seen from this table that the ash-constituents are very generally distributed but occur in varying proportions in different

plants and different parts of the same plant. The difference brought out by the table in the proportions of the more important phosphoric acid and of the less essential silica and lime contained in Rye and Pea seeds, as compared with the amounts of the same substances in the straw, is worthy of notice. The Potato contains much K_2O and little CaO, while the wood of Spruce shows the opposite condition.

Plants.	Ash in 100 parts of dry solid matter.	100 parts of ash contain									
		K_2O	Na_2O	CaO	MgO	Fe_2O_3	Mn_3O_4	P_2O_5	SO_3	SiO_2	Cl
Rye (grain) . .	2·09	32·10	1·47	2·94	11·22	1·24	..	47·74	1·28	1·37	0·48
Rye (straw) . .	4·46	22·56	1·74	8·20	3·10	1·91	..	6·53	4·25	49·27	2·18
Pea (seeds) . .	2·73	43·10	0·98	4·81	7·99	0·83	..	35·90	3·42	0·91	1·59
Pea (straw) . .	5·13	22·90	4·07	36·82	8·04	1·72	..	8·05	6·26	6·83	5·64
Potato (tubers).	3·79	60·06	2·96	2·64	4·93	1·10	..	16·86	6·52	2·04	3·46
Grape (fruit). .	5·19	56·20	1·42	10·77	4·21	0·37	..	15·58	5·62	2·75	1·52
Tobacco (leaves)	17·16	29·09	3·21	36·02	7·36	1·95	..	14·66	6·07	5·77	6·71
Cotton (fibres) .	1·14	36·96	13·16	17·52	5·36	0·60	..	10·68	5·94	2·40	7·60
Spruce (wood) .	0·21	19·66	1·37	33·97	11·27	1·42	22·96	2·12	2·64	2·73	0·07

In the preceding table the figures do not express absolutely constant proportions, as the percentage of the constituents of the ash of plants varies according to the character of the soil.

The mineral substances which form the ash were at first regarded as accidental impurities of the organic substance of the plant. But every attempt to obtain a plant free from mineral substances shows that they form essential constituents.

It was first asserted by BERTHOLLET (1803), and afterwards emphasised by KARL SPRENGEL (1832), and later by LIEBIG, that the mineral salts contained in plants were essential constituents of plant food. Conclusive proof of this important fact was first obtained in 1842 by the investigations of WIEGMANN and POLSTORFF.

This conclusion can be reached by two methods, which at the same time show whether all or only certain of the substances in the ash are necessary. The first method is to cultivate the plant in an artificial soil composed of insoluble substances such as platinum, pure carbon, pure quartz, with which the substances to be investigated can be mixed. The second method, that of WATER CULTURE, is more convenient. Many plants are able to develop their root-system in water instead of in the earth. It is thus possible to add to the water the elements found in the ash in various combinations, and so to ascertain which elements are necessary and which superfluous. As Fig. 245, *I*, shows, the plant (Buckwheat) succeeds well in such a food solution if of suitable composition; it can form roots, shoots, flowers, and fruits, and increase its dry weight a hundredfold or a thousandfold, just as if it were growing in the soil. In distilled

water, on the other hand, while the plant begins to grow normally, the growth soon ceases entirely, and only a very dwarfed plant is produced.

Culture solutions of various composition are used [19a]. KNOP'S solution contains—water 1000, calcium nitrate 1, magnesium sulphate 0·25, acid potassium phosphate 0·25, potassium nitrate 0·25, and a trace of ferric chloride. The solution of V. D. CRONE, with almost completely insoluble compounds of phosphoric acid and iron, appears in some cases to give better results (water 1000, potassium nitrate 1, potassium sulphate 0·5, magnesium sulphate 0·5, tertiary potassium phosphate 0·25, ferrous phosphate 0·25).

From such water cultures it results that the typical land plant succeeds satisfactorily if supplied with the elements K, Ca, Mg, Fe, and H, O, S, P, N, if in addition O and C (the latter as carbon dioxide) are available in the atmosphere. There are thus in all ten elements which must be regarded as indispensable food-materials. Of these the seven which remain after excluding H, O, and C concern us here, since the plant obtains them as nutrient salts from the soil or water. Six of these seven are found in the ash, while the nitrogen escapes on combustion in the form of volatile compounds. That these seven elements are completely indispensable is shown by the fact that if a single one is wanting its loss cannot be made good by an excess of the others, or by the presence of a related element.

FIG. 245.—Water cultures of *Fagopyrum esculentum*. *I*, In nutrient solution containing potassium; *II*, in nutrient solution without potassium. Plants reduced to same scale. (After NOBBE.)

Thus, for example, potassium cannot, as a rule, be replaced by sodium, lithium, or rubidium. Lower organisms (Algae, Bacteria, Fungi) are able to do without Ca. The absence of a single necessary element is shown either by the feeble and dwarfed development of the plant (Fig. 245, *II*, absence of potassium) or by characteristic changes in the plant. The best known of these is the effect of absence of iron, in which case the plant does not become green (chlorosis). Injurious effects of poisoning are shown when calcium is lacking.

More accurate consideration shows that it is not correct to speak of definite elements which are indispensable to the plant. Just as a

mixture of the elements H and O is not a substitute for water, it is not sufficient to supply the plant with the elements contained in the nutrient salts either as elements or in any of their combinations. Thus metallic potassium or pure sulphur are of no use. The plant requires particular salts or, since these in part dissociate in water, particular ions. Necessary kations are K^+, Ca^{++}, Mg^{++}, Fe^{++} (or Fe^{+++}), while SO_4^{--}, $H_2PO_4^-$ and NO_3^- are necessary anions. While phosphorus and sulphur can only be utilised in these combinations, the nitrogen can also be obtained, although not always so usefully in the form of the kation NH_4^+.

The method of water culture has not only shown the necessity for certain salts, but also that many substances, especially sodium, chlorine, and silicon, which the plant usually absorbs can be done without.

Even in halophytes, in which it is present in greatest quantity, sodium is not indispensable. These plants live in soils rich in sodium chloride not because this substance is necessary to them but because they bear it better than other plants do. The concurrence of these in such localities is thus prevented. The characteristic succulent construction of halophytes (Fig. 195) is more or less completely lost in the absence of common salt. Sodium appears to be indispensable to the Diatoms and some Seaweeds ([20]).

Silicon is not indispensable to *Equisetum* and Grasses which contain considerable quantities of SiO_2; on the other hand, it is requisite to the Diatoms, the cell walls of which are almost entirely composed of silicic acid, and owe their permanence to this. The cell walls of Diatoms form considerable geological deposits of siliceous earth or kieselguhr. Aluminium ([21]), while generally distributed in small quantities, is only absorbed in considerable amount by a few plants (*e.g.* species of *Lycopodium*); whether useful or indispensable to these is not established. On the other hand, although scarcely a trace of iodine can be detected by an analysis of sea-water, it is found, nevertheless, in large quantities in seaweeds, so much so that at one time they formed the principal source of our supplies of this substance. Whether it is essential to these plants is not known.

The substances which, as culture experiments show, are not indispensable for the life of the plant are, however, of use in so far as they can replace for some purposes (such as the neutralisation of free acids, etc.) essential elements of plant food. The latter are thus available for the special purposes for which they are indispensable. Thus K can be partially replaced by Na, and Mg by Ca. Certain other substances, although not indispensable, are of use in the plant economy and of advantage to growth. For example, Buckwheat flourishes better when supplied with a chloride, and the presence of silica is advantageous as contributing to the rigidity of the tissues. It has also been found that the presence of certain substances which are not of direct use may inhibit the poisonous action of other substances some of which are necessary.

Absorption of Nutrient Salts.—The nutrient salts can only be absorbed by the superficial cells of the plant when in solution. The question has to be considered in what way the dissolved substances reach the vacuole through the cell wall and the protoplasm. It was seen in connection with plasmolysis (p. 226) that the protoplasm is semi-permeable, *i.e.* permeable to water but not to dissolved substances.

If the protoplasm were really quite impermeable to the salts that have been considered above, not even traces of them could enter the cell cavity. Practically, however, the impermeability of the protoplasm is perhaps not absolute for any substance; there are all grades, from substances that pass through the protoplasm as easily as water, to those that are almost incapable of passing through it. Alcohol, ether, chloral hydrate, numerous organic pigments, and, lastly, very dilute acids and alkalies, diffuse with special rapidity.

The permeability of the protoplasm is not always the same, and may be regulated according to the requirements of the cell ([22]). The salts of alkalies, for example, determine an increasing impermeability as regards themselves, and the salts of the alkaline earths can also diminish permeability for the alkaline salts. The absorption or not of a substance is determined not by the whole protoplasm but by its external limiting layer. In the further passage of the substance, from the protoplasm into the cell sap, the wall of the vacuole exercises a similar power of selection. The cause of the SELECTIVE POWER, by reason of which different cells can appropriate quite distinct constituents or substances in different amounts from the same soil, is to be sought in this most important property of the limiting layers of the protoplasm.

From the same soil one plant will take up chiefly silica, another lime, a third common salt. The action of Seaweeds in this respect is especially instructive; living in a medium containing some 3 per cent of common salt and poor in potassium salts, their cells, nevertheless, absorb relatively little common salt, but accumulate potassium salts.

Every substance to which the limiting layers of the protoplasm are permeable must ultimately reach the same concentration in the vacuole as in the solution outside the cell when its absorption would cease. Practically it often enters in much greater amount than this. Thus, for example, only a trace of iodine is present in sea-water, but may be accumulated in such quantities in seaweeds for these to become a source from which it is commercially obtained. The cell has not only a selective power, but is also able to store up materials by converting them into insoluble or indiffusible forms.

Certain organic pigments ([23]) such as methylene blue are especially suited to demonstrate the entrance and accumulation. Many cells contain tannins in their vacuoles, and these substances form with the entering pigment a compound which is indiffusible or quite insoluble. For this reason the vacuole becomes deeply coloured or has blue precipitates, though the solution of methylene blue employed is extremely dilute. It is noteworthy that the protoplasm itself remains unstained and is not in any way injured; the pigment would be accumulated in dead protoplasm.

Under natural conditions some plants absorb the nutrient salts from water as do the plants in a water-culture experiment. This is

the case in many water plants in which the whole external surface is of use in absorption. Since the salts only exist in very dilute solution in the water, the need of an extended surface for this purpose is readily understood; this in part explains the frequent occurrence of finely divided leaves in water plants. The salts dissolved in the water are not, however, sufficient for all aquatic plants; many absorb substances from the soil underlying the water by means of their roots, and do not succeed when deprived of roots.

As a rule in the higher plants the salts are absorbed from the soil. The salts contained in the nutrient solution described above, or similar compounds, are constantly present in the water of the soil; some of them, however, in such small amount as only to suffice for the growth of plants for a short period. Other sources of supply of the food-salts must exist when such growth continues. In fact, the amount of salts dissolved in the soil-water is no measure of the fertility of the soil. The soil always contains food-salts, partly in an absorbed condition, and partly in mineral form which the plant has to render accessible. This is effected mainly by the excretion of carbonic acid from the root-hairs. Many substances are much more readily soluble in water containing carbonic acid than in pure water.

The solution of solid rock by the plant may most readily be shown by allowing the roots to grow against smooth polished slabs of marble; the course of the roots is indicated by the etching of the surface.

There are other cases in which stronger acids than carbonic acid excreted by the plant are concerned in bringing minerals into a soluble form. This can hardly be doubted when felspar and mica are dissolved by certain Lichens ([24]). Fungi and Bacteria also frequently produce and excrete solvents of this kind during their metabolism, and may have a similar effect on insoluble substances in the soil.

Some soils, especially those containing much clay, lime, or humus, have the property of retaining potassium and ammonium salts, and in less degree salts of calcium and magnesium, as well as phosphates; these substances are not easily washed out of the soil but can be obtained by plants. This is spoken of as the power of absorption of the soil for the substances in question. This does not hold for all salts; thus, for instance, sulphates and nitrates are not absorbed. Absorption is completely wanting in a pure sandy soil.

When the substratum contains, in addition to water and nutrient salts, dissolved organic substances, these may be absorbed in the same way. Water cultures show, however, that at least the typical green plant is not dependent on such substances. It is otherwise with the Fungi and other plants which resemble them in metabolism (p. 255).

In addition to water and nutrient salts dissolved gases may also be absorbed by the roots. As a rule only oxygen need be considered. The main source from which gases are absorbed is the atmosphere.

Transport of the Nutrient Salts.—The salts do not remain in the epidermal cells of the root or shoot but pass from the place of absorption through the whole plant. This takes place in two ways,

by DIFFUSION and by CONDUCTION. Necessary conditions for diffusion are that the cell wall and protoplasm should be permeable for the substance in question, and that there should be a difference in its concentration between the starting place and termination. In the transport from one vacuole to that of the neighbouring cell the substances must first pass into the protoplasm, then into the cell wall, then again into the protoplasm, and finally into the vacuole. The cell walls, at all events when thick, appear to offer special difficulty in the process. On this account all thickened cell walls are provided with thin places (pits), and the pit membranes are traversed by fine protoplasmic threads (plasmodesms, p. 44). In the sieve-tubes the pit membrane is absorbed, and thus coarser strands of protoplasm connect the one cell with its neighbour. The investigations of BROWN and ESCOMBE have shown that a finely perforated septum, if the perforations are a certain distance apart, offers no obstacle to diffusion ([25]).

Movements of diffusion may also take place within a cell if dissolved substances are not at the same concentration throughout the cell. Movements of diffusion proceed quite slowly. The rapidity with which mixing occurs may be greatly hastened if a movement in mass be added to that due to diffusion. In common life and in the laboratory this is effected by shaking the solution, and within a cell the same result may be obtained, *e.g.* by the protoplasmic movements. The greater the length of a cell the more suitable is it for conducting material through the plant, since the slow diffusion movement need only take place at long intervals, *i.e.* at the ends of the cell; in the intermediate portion movements of mixing play a large part.

When a plant requires more rapid transport of materials the nutrient salts are conveyed in the plant by the transpiration current. It is thus not merely water but a very dilute food-solution that is conducted by the vascular bundles, and the use of transpiration is, in the first place, to concentrate this nutrient solution and, in the second, to bring it quickly to the proper parts of the plant. Apart from this result it would be difficult to understand the process of transpiration, and the plant would certainly have found means of limiting it. When it is actually checked (cf. p. 168), we have to do with plants which grow slowly on account of the poor supply of salts, and also it is true of carbonic acid.

Nutrient Salts and Agriculture.—Since the plant thus continues to absorb nutrient salts from the soil, this must become poorer in the particular substances unless the loss is repaired in some way. In nature this results from the fallen and dead parts of plants returning to the soil, and the salts contained in them becoming available for further life. In agricultural practice, however, a large proportion of the vegetation is removed in the crop, and the salts it contains are thus lost to the ground; at the most a fraction may be returned to

the soil in the dung of grazing animals. The effect of manure in increasing growth, which has for ages been known to practical men, depends at least in part on the salts contained in it. Since, however, the amount of salts thus returned to the soil is insufficient to meet the loss, artificial manuring is required in agricultural practice ([26]). The first place among manures must be given to those which contain nitrogen, potassium, and phosphoric acid. Nitrogenous substances which are used besides guano (which also contains phosphoric acid) are Chili saltpetre, ammonium sulphate, calcium cyanamide, and calcium nitrate; the two last have recently been artificially prepared from atmospheric nitrogen. Potassium is present in the Stassfurt waste salts, of which kainite is the most important since it also contains $MgSO_4$. As an important source of phosphorus, the so-called Thomas slag may be mentioned; this substance is formed in working ores containing phosphorus, and consists of triple phosphate of calcium. It can only be utilised by plants when in a state of very fine subdivision, as what is known as "Thomas-meal." Superphosphate is obtained by the treatment of potassium phosphate with sulphuric acid.

The Soil and Plant Geography.—From what has been said it might be concluded that a soil capable of supporting one kind of plant must be able to support any other species. Plant geography ([27]), however, shows that the composition of the soil exerts a great influence on the distribution of plants. This depends, on the one hand, on the fact that different plants make different demands on the amount and solubility of the essential food-materials, and, on the other, upon the presence in the soil of substances other than the indispensable salts; the influence of these non-essential substances is different upon different species of plants. For example, $CaCo_3$ has a poisonous effect on some plants, and NaCl upon others, while other plants can endure large doses of these substances.

The effect of the soil upon the distribution of plants does not depend merely upon its chemical nature. The physical properties of soils play an important rôle. Further, a plant may be absent from a locality, which, so far as the nature of the soil is concerned, would be suitable, because its seeds have never been brought to the spot.

(c) Gases

While water and salts are, as has been seen, as a rule absorbed from the soil, the air contains substances which are necessary to the successful existence of the plant, and must be termed food-materials. These are carbon dioxide and oxygen. They are, as a rule, obtained from the atmosphere. Only submerged water plants obtain them from the water, in which case they are absorbed in the same way as other dissolved substances.

Oxygen.—When a plant is deprived of oxygen, all vital manifesta-

tions usually cease. Since oxygen is also essential to the human organism, this fact does not seem surprising (cf. p. 273).

Carbon Dioxide.—It appears at first sight much less self-evident that carbon dioxide should be indispensable to the plant, and yet this is the case. While no source of carbon is offered to the plant in a water culture, it grows in the food-solution, and accumulates carbon in the organic compounds of which it consists; the only possible conclusion is that the plant has utilised the carbon dioxide of the atmosphere. Carbon dioxide is present in ordinary air in the proportion of 0·03 per cent. If such air is passed over a green plant exposed to bright light, it can be shown that the carbon dioxide diminishes in amount or disappears. Colourless parts of the plant, or organisms like the fungi which are not green, behave differently; they absorb no carbon dioxide. If a green plant is placed in a bell-jar and supplied with air freed from carbon dioxide, its growth soon stops, and increase in dry weight ceases completely. Carbon dioxide is thus an indispensable food-material, and is evidently the source from which the plant obtains its carbon. The small proportion of this gas present in the atmosphere is quite sufficient for the nutrition of plants (p. 251). A supply of organic compounds of carbon in the soil or culture solution does not enable a plant to dispense with the carbon dioxide of the air; in any case CO_2 is the best source of carbon for the green plant which we are at present considering. Neither is it sufficient to supply such a plant with carbonic acid in the soil or culture solution; it requires to be supplied directly to the leaves.

Other Gases.—Oxygen and carbon dioxide are the only gases which are necessary to the plant. For most plants the nitrogen of the atmosphere is of no use (cf. p. 259).

Absorption of Gases.—Carbon dioxide and oxygen in part enter the epidermal cells, and partly pass by way of the stomata into the intercellular spaces, from which they reach the more internal tissues.

There are no air-filled canals or spaces in the cell wall or the protoplasm through which gases could diffuse into the cell. Thus absorption of gases is only possible in so far as they are soluble in the water permeating the protoplasm and wall. The gases behave like other dissolved substances and diffuse into the cell. They diffuse through cell walls more easily the richer in water these are. The ordinary cell wall, when in a dry condition, hardly allows gases to diffuse through it ([28]); in nature, however, the cell wall is always more or less saturated with water. The cuticle, on the other hand, has very little power of imbibing water, and places considerable difficulty in the way of any diosmotic passage of gases; it is not, however, completely impermeable.

The gaseous diffusion takes place rather through the substances with which the cell wall is impregnated than through the substance of the wall itself. Since carbon dioxide is much more readily

soluble in water than is oxygen, it will be evident that it will pass more rapidly through a cell wall saturated with water than oxygen will. In all probability this holds for the cuticle as well. Since, however, the partial pressure of the oxygen in the air is relatively considerable, while that of carbon dioxide is very slight, oxygen can pass in sufficient quantity through the cuticle, but carbon dioxide cannot; on this account we find that all organs which only require to absorb oxygen are unprovided with stomata, while organs which absorb carbon dioxide always have stomata.

In the soil as well as in the air, plants, as a rule, find so much oxygen that this gas is able to pass through the epidermis. Organs which live in swampy soil which is poor in oxygen form an exception to this. In marsh plants, which stand partly in the air, the large intercellular spaces form connecting canals through which the atmospheric oxygen without being completely used up can reach the organs growing deep in the swampy soil and cut off from other supplies of oxygen. In some cases (especially in Palms and Mangroves) the need of a supply of oxygen to such roots is met by specialised roots (PNEUMATOPHORES) which project vertically from the muddy soil (Fig. 188), and absorb oxygen from the air.

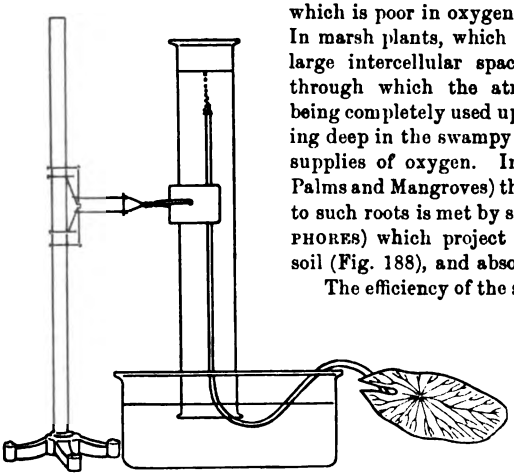


FIG. 246.—Diagram of an experiment to demonstrate the movement of air through the stomata.

The efficiency of the stomata in gaseous exchange varies with the width to which the pores are open. The closure of the pores of the stomata, which may be brought about in maintaining a sufficient supply of water, not only arrests transpiration, but also prevents the entrance of CO_2 into the plant.

It has been seen in considering the giving off of water vapour that the stomata in spite of their small size facilitate diffusion on account of their enormous numbers and their distribution. This also applies to the absorption of carbon dioxide. Thus, for example, a square metre of the surface of a *Catalpa* leaf absorbs about two-thirds the amount of carbonic acid gas taken up in an equal time by the same area of potash solution freely exposed to the air.

The Movement of Gases from cell to cell and their interchange between the cells and the intercellular spaces takes place by diffusion. In the intercellular spaces movements in mass due to pressure are concerned. Unequal pressure is set up by the warming or cooling of the air in the intercellular spaces, or by movement of the part of the plant leading to changes of shape. The intercellular spaces form a highly-branched system of cavities communicating with one another and with the atmosphere. The communication with the outside is effected in the first instance by the stomata, and also by the lenticels

and organs of similar function (p. 59); both diffusion and movements in mass of the gases go on through these openings.

That the intercellular spaces were in direct communication with each other, and also with the outer atmosphere, was rendered highly probable from anatomical investigation, and has been positively demonstrated by physiological experiment. It is, in fact, possible to show that air forced by moderate pressure into the intercellular passages makes its escape through the stomata and lenticels; and conversely, air which could enter only through the stomata and lenticels can be drawn out of the intercellular passages. The method of conducting this experiment can be seen from the adjoining figure (Fig. 246). The leaf-stalk of an uninjured leaf of *Nymphaea* is introduced into a glass cylinder which has been filled with and inverted in water. The leaf-blade is under atmospheric pressure; the pressure on the cut end of the petiole is less than this by a few centimetres of water. This difference is, however, sufficient to maintain an active current of air from the cut petiole. That this air enters by the stomata is shown by the stream ceasing when the upper surface of the leaf is submerged and the stomata thus cut off from the air.

Intercellular air-spaces are extensively developed in water and marsh plants (cf. p. 165), and may form two-thirds of their volume. The submerged portions of water plants unprovided with stomata thus secure a special internal atmosphere of their own, with which their cells maintain an active interchange of gases. This internal atmosphere is in turn replenished by slow diffusion with the gases of the surrounding medium. As regards the rest of their gaseous interchange, these plants are wholly dependent on processes of diffusion, since stomata, etc., are wanting. Plants which possess these organs may also obtain gases by diosmosis if the cuticle of their epidermis is permeable to gases.

III. The Assimilation of the Food-Materials

The plant grows and continues to form new organs; for these purposes it continually requires fresh supplies of food-materials. The materials of the food become changed after their absorption, and the substance of the plant is built up from them. They are said to have been ASSIMILATED. By assimilation is understood the transformation of a food-material into the substance of the plant. Those processes of assimilation in which profound changes take place, *e.g.* the change from inorganic to organic compounds, are especially interesting. This is particularly the case when we are still unable to experimentally bring about the reaction outside the organism.

A. ASSIMILATION OF CARBON

1. Assimilation of Carbon Dioxide in Green Plants

The assimilation of carbon dioxide by a green plant is a process of the kind referred to in which organic substance containing carbon is derived from carbon dioxide. In the assimilation of carbon dioxide, soluble carbohydrates such as grape-sugar are formed in the chloroplast under the influence of sunlight. If we assume that the carbonic

acid gas of the atmosphere (carbon dioxide, CO_2) becomes on its solution in the cell H_2CO_3, the formation of sugar would take place in two stages. In the first, oxygen would be given off and formaldehyde ([28a]) formed :

$$H_2CO_3 = H_2CO + O_2.$$

In the second stage the aldehyde is polymerised to sugar :

$$6H_2CO = C_6H_{12}O_6.$$

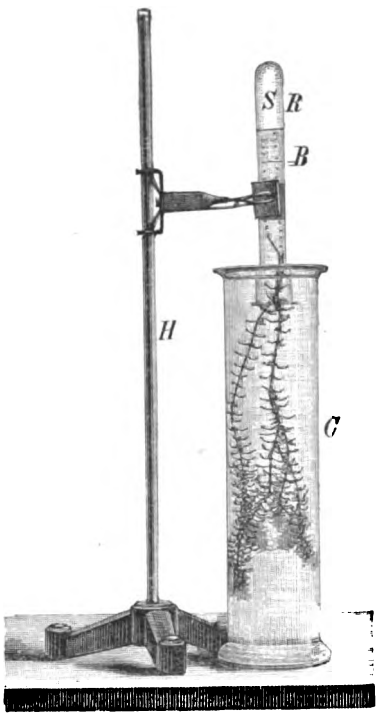


FIG. 247.—Evolution of oxygen from assimilating plants. In the glass cylinder *C*, filled with water, are placed shoots of *Elodea canadensis* ; the freshly-cut ends of the shoots are introduced into the test-tube *R*, which is also full of water. The gas bubbles *B*, rising from the cut surfaces, collect at *S*. *H*, stand to support the test-tube. (After NOLL.)

In any case, for every volume of carbon dioxide which disappears an equal volume of oxygen makes its appearance. It has been shown by eudiometric measurements that this is the case (WILLSTAETTER). The oxygen given off can, however, even when it is only detected qualitatively, be used as an indicator of the decomposition of the carbonic acid. Thus, when a plant is enclosed along with phosphorus in a space free from oxygen and exposed to light, the formation of oxygen is shown by the white fumes given off from the phosphorus. Another means of drawing conclusions as to the production of oxygen by a green plant is afforded by the movements of certain Bacteria which previously lay motionless in the water (p. 331). The clearest demonstration of assimilation is obtained by using certain water plants such as *Elodea* or *Potamogeton*. If cut shoots or leaves of these plants are submerged in water and exposed to light, a brisk continuous stream of bubbles comes from the cut surface. If the gas is collected in considerable quantity in a suitable apparatus, *e.g.* in a test-tube (Fig. 247), it can be shown to consist not of pure oxygen but of a mixture of gases rich in oxygen ; a glowing splinter bursts into flame in the gas.

The appearance of the bubbles of oxygen is explained in this way. The carbon dioxide dissolved in the water enters the green cells of the plant by diffusion and is there decomposed. The oxygen given off is much less soluble than carbon dioxide and therefore appears in the gaseous form. It passes into the intercellular spaces,

causing there an increase of the pressure, and this is the cause of the appearance of bubbles of gas at every wounded surface.

The foundations of our knowledge of the assimilation of carbon dioxide by the green plant were laid, in the end of the eighteenth and beginning of the nineteenth centuries, by PRIESTLEY, INGENHOUSS, SENEBIER, and TH. DE SAUSSURE. The discovery is of extraordinary significance, for THE FORMATION OF ORGANIC MATERIAL FROM CARBON DIOXIDE BY THE GREEN PLANT IS THE PROCESS WHICH RENDERS POSSIBLE THE LIFE OF ALL OTHER ORGANISMS AND IN PARTICULAR OF ANIMALS UPON THE EARTH (cf. p. 255).

By means of the gas-bubble method it is easy to bring proof of the statement made above that only the green parts of plants, and these only in light, are able to assimilate CO_2. Thus the stream of bubbles from an *Elodea* which goes on briskly at a brightly-lit window becomes slower as the plant is brought into the middle of the room, and ultimately ceases when the intensity of the light is

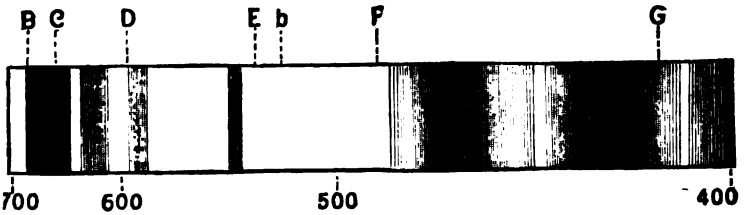


FIG. 248.—Absorption spectrum of chlorophyll according to GR. KRAUS. The Fraunhofer lines (B, C, etc.) are indicated above and the wave-lengths (700 $\mu\mu$–400 $\mu\mu$) below. The black and shaded regions are those where the light is absorbed or weakened.

still such as to allow our eyes to read. Within certain limits assimilation increases in proportion to the intensity of the light. Similar experiments may be carried out using artificial sources of light. They show that all the methods of illumination in common use may be effective in the assimilation of CO_2. The rays of different wave-length are by no means of equal use in assimilation.

The ultra-red and ultra-violet rays have very little effect, and the assimilatory activity is almost entirely limited to the rays of a wave-length from about 0·4 μ to 0·8 μ which are perceived by our eyes. Within these limits light of a wave-length of about 0·68 μ has undoubtedly the greatest effect; this is the wave-length at which the maximum absorption of light by chlorophyll occurs (Fig. 248). In other regions of the spectrum also, according to URSPRUNG, there is a correspondence between the absorption of light and assimilation. It is true that the assimilation in blue and violet light is not so great as the absorption bands would suggest; according to URSPRUNG this depends on secondary causes.

Since sunlight is in nature an indispensable factor in CO_2 assimilation it becomes at once clear why certain organs of the plant, the foliage leaves, have a flat expanded shape. Their large surface fits

them to absorb the light. If their function of CO_2 assimilation is to be well performed the foliage leaves must not only have a large surface but also be thin. Practically it appears that light which has passed through one or two foliage leaves is unable to exert any further assimilatory effect. The leaves must, however, contain a very large number of chlorophyll grains. Their dark green colour shows that this is the case, and microscopical examination confirms this. Stems have far fewer chloroplasts than the leaves, and the roots and other subterranean organs have none at all.

Every investigation shows that organs without chlorophyll are quite unable to assimilate carbon dioxide. This holds not only for the organs of the plant but for the parts of the cell. The colourless protoplasm and the nucleus of the cell give off no oxygen when exposed to sunlight; this can readily be proved by the bacterial method (p. 248). The chloroplasts alone are the active organs in CO_2 assimilation, and only when they contain chlorophyll; etiolated or chlorotic chloroplasts are not functional.

In the red-leaved varieties of green plants, such as the Purple Beech and Red Cabbage, chlorophyll is developed in the same manner as in the green parent species, but it is hidden from view by a red colouring matter in the epidermis or in deeper-lying cells. In the Red Algae, on the other hand, the chromatophores themselves have a red colour; after death a red pigment (phycoerythrin) becomes free, leaving the chloroplasts green. Regarding the pigments in the Phaeophyceae and the Diatomeae cf. p. 19.

In studying the effect of different kinds of light upon assimilation, it is customary either to use the separate colours of the solar spectrum, or to imitate them by means of coloured glass or coloured solutions. SCHOTT and others have employed red and blue glasses or double-walled bell-jars filled with suitably-coloured solutions.

Only a relatively small percentage of the light which falls on the leaf and is absorbed is utilised in the assimilation of CO_2 ([29]). That, however, light must disappear as such in CO_2 assimilation is clear, for from what other source than the energy of light could the energy be obtained that is stored up in the organic substance formed in assimilation? This potential energy of the organic substance of the plant serves to maintain the vital processes. The force exerted by our steam-engines is also to be traced to the assimilatory activity of the plants, the wood or the carbonised remains of which are burnt beneath its boiler. In the combustion of the reduced carbon compounds to carbon dioxide the energy, which was previously required to transform carbon dioxide into the combustible materials, again becomes free.

The assimilatory activity of a chloroplast, like every vital function, is dependent on a number of internal and external factors. To the internal factors belong the presence of the pigment chlorophyll and its situation in a living chloroplast. Chlorophyll itself, separated from

the plant, is as little able to decompose the carbon dioxide as is a chloroplast which for any reason has not developed the characteristic pigment (chloroplasts developed in the dark or in the absence of iron, leucoplasts of subterranean parts or of epidermal cells) or has lost it (chromoplasts). Since, however, assimilation is not proportional to the amount of chlorophyll, it is necessary to assume with WILLSTAETTER ([30]) that in addition to the pigment another factor is essential, whether this is the protoplasm of the chloroplast or an enzyme which it contains (p. 264).

Among external factors sunlight as referred to above must be mentioned first, and next the presence of carbon dioxide. Since the latter is only present in small proportion in the air, the life of plants, and with this the existence of all organisms, would ultimately cease were not fresh supplies of carbon dioxide continuously produced. Estimating the amount of carbon dioxide in the atmosphere at 2100 billion kilogrammes and the annual consumption by green land plants at 50-80 billion kg., the supply would be used up in some thirty years ([30a]).

The air is continually receiving new supplies of carbonic acid through the respiration and decomposition of organisms, through the combustion of wood and coal, and through volcanic activity. An adult will exhale daily about 900 grammes CO_2 (245 grammes C). The 1400 million human beings in the world would thus give back to the air 1200 million kilos of CO_2 (340 million kilos C). The CO_2 discharged into the air from all the chimneys on the earth is an enormous amount. In Germany alone in 1911, besides 73 million tons of brown coal, 161 million tons of coal were used; the latter would produce some 400,000 million kg. of carbon dioxide, which is about 1/5000 of the total amount in the atmosphere. Animals produce large amounts of carbon dioxide in respiration, as also do plants, including fungi and bacteria (especially the bacteria of the soil).

The fixation of carbon dioxide by green plants and the production of carbon dioxide in the ways referred to are approximately equivalent. The amount of carbonic acid gas contained in the air varies at different times and places. It has been found that in 10,000 litres of air it was 2·7 to 2·9 litres in July, 3·0-3·6 litres in the winter; close to the ground 12-13 litres were present in the same volume. The average amount is about 3⅓-3½ litres in 10,000 litres of the atmosphere. This weighs about 7 grammes, of which $\frac{8}{11}$ is oxygen, and only $\frac{3}{11}$ carbon. Only 2 grammes of carbon are thus contained in the 10,000 litres of air. In order, therefore, for a single tree having a dry weight of 5000 kilos to acquire its 2,500,000 grammes of carbon, it must deprive 12 million cubic metres of air of their carbonic acid. From the consideration of these figures, it is not strange that the discovery of INGENHOUSS was unwillingly accepted, and afterwards rejected and forgotten. LIEBIG was the first in Germany to again call attention to this discovery, which to-day is accepted without question. The immensity of the numbers just cited are not so appalling when one considers that, in spite of the small percentage of carbonic acid in the atmosphere, the actual supply of this gas is estimated at about 2100 billion kilos, in which are held 560 billion kilos of carbon. The whole carbon supply of the atmosphere is at the disposal of plants, since the CO_2 becomes uniformly distributed by constant diffusion.

Submerged water plants absorb the CO_2 dissolved in water. Its amount varies

considerably according to the temperature. At 15° C. a litre of water contains about as much CO_2 as a litre of atmospheric air. The dissolved bicarbonates also play an important part in the supply of carbon to aquatic plants [31].

Artificially conducting carbonic acid through the water increases, to a certain degree, the evolution of oxygen, and the assimilatory activity. Similarly an artificial increase of carbonic acid in the air is followed by increased assimilation. Whether and to what extent an artificial enriching of the air in CO_2 would be of advantage in horticulture or agriculture cannot be said [32].

The CO_2 assimilation, like all vital processes, is dependent on the temperature. It begins at a temperature a little above zero, reaches its maximum at about 37° C., and again stops at about 45° C.

These cardinal points not only have different positions in different plants but do not remain constant for any particular plant. This is especially true of the optimum which in the course of a few hours may sink from 37° C. to 30° C. In bright warm weather assimilation does not reach its full possible value since the supply of carbon dioxide is then insufficient.

Other less important factors need not be considered in detail. It may be mentioned, however, that many substances can bring about a temporary, or ultimately a permanent, limitation or arrest of the assimilatory process.

Products of the Assimilation of Carbon Dioxide.—It was assumed above that sugar was formed from the carbon dioxide, and analysis in fact shows that the amount of sugar in a foliage leaf is increased after exposure to sunlight. It is true that grape-sugar is neither always nor only shown to be present; usually other more complex carbohydrates appear. These can all, however, be traced back to hexoses like grape-sugar, and arise by the union of two or more molecules of hexose and the loss of the elements of water. Prominent among them are cane-sugar ($C_{12}H_{22}O_{11}$) and starch $(C_6H_{10}O_5)_n$. The occurrence of starch in the chloroplasts of illuminated foliage leaves is very common, but by no means general. When the leaves are placed in darkness for some time the starch disappears. When on the other hand a part of the plant from which the starch has been removed is exposed to sunlight, new starch grains often form in the chloroplasts in a surprisingly short time (5 minutes); these soon increase in size and ultimately exceed in amount the substance of the chloroplast itself. Since starch is stained blue by iodine the commencement of assimilation can be readily demonstrated macroscopically (SACHS' method).

Leaves which have been in the light have their green colour removed by means of alcohol, and are treated with a solution of iodine; they take on a blue colour. If the amount of starch is greater the colour is a deeper blue or almost black. The depth of the coloration thus affords a certain amount of information as to the quantity of starch present. To demonstrate smaller amounts of starch the decolorised leaves are placed, before staining with iodine, in a solution of potash or of chloral hydrate in order to swell the starch grains. This method of demonstrating assimilation can also be used to show that the starch only appears in the illuminated portions of the leaf. If a stencil of opaque material from which, for instance, the word "Stärke" has been cut is laid on the leaf, the word "Stärke"

will appear blue on a light ground, as in Fig. 249, when the leaf after being illuminated is treated with iodine. Instead of a stencil a suitable photographic negative can be used, as MOLISCH has shown; after illumination and subsequent treatment with iodine a positive photograph is obtained (Fig. 250).

In some plants (many Monocotyledons) no starch is formed in the chloroplasts, but the products of assimilation pass in a dissolved state directly into the cell sap. Starch is formed, however, where there is a surplus of glucose, sugar, and other substances, as, for example, in the coloured plastids of flowers and fruits. The guard cells of the stomata and the cells of the root-cap of these Monocotyledons also contain starch. In other cases only a fraction of the product of assimilation appears as starch (in *Helianthus*, for example, only $\frac{1}{8}$), while the rest remains as sugar or is otherwise made use of. It is thus clear that the amount of starch formed cannot always be taken as a measure of the assimilation.

Starch formation can be induced to take place in the dark by floating leaves on a sugar solution of suitable concentration. This shows that the formation of starch does not stand in direct connection with the assimilation of carbon dioxide but is only the result of the accumulation of sugar in the cell.

FIG. 249. — Assimilation experiment with the leaf of *Ariopsis peltata*. (Reduced.)

FIG. 250.—The positive photograph obtained by covering a leaf of *Tropaeolum* which has been freed of starch by the negative and exposing it to the sun. After assimilation the leaf has been treated with iodine. (After MOLISCH.)

In some Algae neither sugar nor starch but other products of assimilation are formed, *e.g.* Floridean starch.

The nature of the "fat-drops" which frequently appear in assimilating cells and their connection with this process is still uncertain ([32a]).

The Quantity of the Assimilated Material depends on the one hand upon the kind of plant and on the other upon the external conditions to which it has been exposed. It can be said that a square metre of leaf of an actively assimilating plant under optimal external conditions produces between 0·5 and 1 gramme of dry substance per hour. When it is considered how many square metres of leaf surface are daily assimilating, a conception can be formed of the huge production of organic substance in this largest of all chemical factories. SCHRÖDER estimates the amount formed annually by land plants

as about 35 billion kg. The German harvest alone contained in 1912 some 9 milliards kilos of assimilated material in the cereals (rye, wheat, spelt, barley).

There are two methods ([33]) in use for determining the amount of assimilation. The method invented by SACHS is as follows. In the morning portions of leaves, usually halves, are removed; their superficial area is measured and they are then dried and weighed. In the evening equally large portions (the remaining halves) of the leaves which have been exposed to light throughout the day are similarly dried and weighed. The increase of weight indicates the gain to the plant by the assimilation of carbon. This is SACHS' half-leaf method. A quite distinct method of quantitatively determining the assimilation of CO_2 is that of KREUSLER which has been used by GILTAY and BROWN. A leaf still attached to the plant is placed in a closed chamber through which a constant current of air passes; the amount of CO_2 removed from the air by the leaf is determined. The amount of sugar or starch which could be formed from this amount of CO_2 can then be easily calculated.

2. The Gain in Carbon by Bacteria ([34])

Certain Bacteria, which will be described in another part of this text-book, are characterised by the power of increasing their substance in a purely inorganic food-solution; they do this in the dark and without chlorophyll so long as carbonates are present. This has been determined for the Nitrite- and Nitrate-bacteria, the Sulphur-bacteria, and for the Bacteria which oxydise methane and hydrogen. Some of them depend entirely on CO_2, while others can also utilise organically-combined carbon.

Nothing is known at present of the products of carbon assimilation in these Bacteria. The gain in organically-combined carbon is slight. Only a quite minimal fraction of the organic carbon compounds which at any moment exist on the earth owes its origin to these Bacteria. The fact of their carbon assimilation remains none the less interesting, especially since it takes place in an essentially different manner to the assimilation of the green plant. Some other source of energy must take the place that sunlight does in assimilation in a green plant to build up the organic substance; this energy is obtained by oxidation of ammonia, nitrites, oxide of iron, sulphuretted hydrogen, methane, and hydrogen (p. 274). We may therefore term the formation of organic material in green plants PHOTOSYNTHESIS, and in these Bacteria a CHEMOSYNTHESIS.

3. The Gain in Carbon in Heterotrophic Plants

While the gain of carbon from carbon dioxide is to be considered as the typical carbon assimilation of plants, it is by no means the only method found in the vegetable kingdom. Since it depends—leaving the Bacteria mentioned above out of account—on the presence of

chlorophyll and of sunlight, it cannot come into consideration in subterranean parts of plants, in all plants that are not green, and in the case of all animals. All these are in fact dependent on organically-combined carbon which has been derived directly or indirectly by the assimilatory activity of green parts of plants. All organisms which in their nutrition are dependent on the activity of green plants are termed heterotrophic; the green plants and also the Nitro-bacteria are termed autotrophic. Autotrophic plants also depend on other organisms. It will be seen that life is only continuously maintained on the earth by the changes in substances effected in one direction by particular organisms being balanced by the activity of other organisms. Heterotrophic organisms show by their mode of life, and especially by the situations in which they live, that they make other demands on food-material than do autotrophic plants. They occur either as parasites on living plants and animals, or they live as saprophytes on dead organisms or substances derived from organisms.

The demands which heterotrophic plants make on a source of carbon can be best studied in saprophytic Bacteria and Fungi. These organisms can be cultivated on various complex substrata, and conclusions can be drawn from their growth as to the nutritive value of the compounds supplied as food. The nutrient solution must as a rule contain, in addition to the indispensable mineral substances and a source of nitrogen (usually a salt of ammonia), sugar as a source of carbon. It should have a slightly acid reaction for mould fungi and be weakly alkaline or neutral for bacteria, and is often converted into a solid medium by mixture with gelatine or agar-agar. The sugar can, in many cases, be more or less suitably replaced by other organic substances such as other carbohydrates, fats, albumen and derived substances, organic acids, etc. While these sources of carbon can be placed in order as regards their nutritive value for any particular organism, this cannot be done generally; there are many saprophytes which are adapted to quite peculiar conditions and use in preference, as a source of their carbon supply, compounds, which for the majority of other plants have scarcely any nutritive value (*e.g.* formic acid, oxalic acid).

Even the saprophytes which succeed on very various compounds of carbon (omnivorous saprophytes) are capable of distinguishing between them. Thus from ordinary tartaric acid *Penicillium* only utilises the dextro-rotatory form, and *Bacillus subtilis* only the laevo-rotatory form. *Aspergillus* growing in a mixture of glucose and glycerine utilises the former first ("election" of nutritive materials). If the glycerine alone is given, it is completely utilised.

The power possessed by many Fungi of utilising such organic compounds as starch, cellulose, etc., which are insoluble in water, is very remarkable; these substances can only be absorbed after a process of transformation and solution. The Fungi and Bacteria in question

excrete enzymes (cf. p. 264), which have the power of rendering the substances soluble.

Saprophytes are thus characterised by the nature of their assimilatory activity; they are unable to carry out the first step in the assimilation of carbon which is effected so easily by the green plant with the help of light. On the other hand, there is probably no difference between them and autotrophic plants in the further steps of assimilation, in the construction from simple organic compounds of the more or less complex compounds which compose the body of the plant.

Among phanerogamic plants also some heterotrophic forms, that at first sight appear to be saprophytes, occur. This is the case for certain orchids which grow in humus (*Neottia*, *Coralliorrhiza*, *Epipogon*) and for *Monotropa*. The absence of chlorophyll and, except for the inflorescence, the subterranean mode of life indicate the heterotrophic nature of these forms. The obvious assumption that they obtain their supply of carbon from the humus of the soil of woods is, however, very improbable. Since all these plants harbour a fungus in their roots or rhizomes, the absorption of food material is probably due to the fungus. The flowering plants probably lead a parasitic life upon the fungi in their roots (mycorrhiza; cf. p. 261).

These plants thus lead us to the consideration of PARASITES, numerous examples of which are found in the Fungi and Bacteria; parasitic forms also occur among Algae, Cyanophyceae, and the higher plants.

That these parasites, or at least many of them, absorb nutrient materials from the host upon which they live is often evident from the condition of the latter; the host may be seriously injured and even ultimately killed by the parasite. What the particular substances are that the parasite absorbs and requires for successful growth is, however, difficult to determine. Since frequently only organisms of a definite natural group (family, genus, species) are attacked by one species of parasite, it may be assumed that the latter makes quite specific demands as to the quality or quantity of its nutriment. This assumption is supported by the fact that we are unable to cultivate most parasites apart from their hosts.

B. Assimilation of Nitrogen

Since a green plant obtains its carbon from carbon dioxide, which is only present in a very small proportion in the air, it might be assumed that the enormous supply of nitrogen in the air would form the primary and the best source of this element of plant food. Every water culture, however, shows clearly that atmospheric nitrogen cannot be utilised by the typical green plant. If combined nitrogen is omitted from the nutrient solution the plant will not grow.

In the food-solution given above nitrogen was supplied as a nitrate, and this form is most suitable for the higher plants. But compounds of ammonia, so long as they are not injurious to the plant owing to an alkaline reaction, can also be utilised. Organic compounds of nitrogen also, such as amino-acids, acid amines, amines, etc., will serve for food, though none of them lead to such good results as are obtained with nitrates. Nitrites can also serve as a source of nitrogen, but in too high concentrations are injurious.

We are not nearly so well acquainted with the assimilation of nitric acid and of ammonia as we are with that of carbon dioxide. We do not know accurately the place in which the assimilation takes place, we know less of the contributory external conditions, and lastly, we are not clear as to the products of assimilation. Ultimately, of course, albumen is formed, a far more complex substance than a carbohydrate, containing always, besides C, H, and O, some 15-19 per cent of N, besides S and in some cases P. The methodical study of the products of the breaking down of albumen gives some insight into the structure of the proteid molecule. This shows that in albumen a large number of amino-acids are combined with loss of water. Since EMIL FISCHER has obtained albuminous substances (polypeptides) by a union of amino-acids followed by polymerisation, it is probable that in the plant also such amino-acids are first formed and then unite further. If the simplest amino-acid, glycocoll, $NH_2 \cdot CH_2 \cdot CO_2H$ (which, it is true, is not of wide occurrence in plants), is considered, it is evident that this can be derived from acetic acid by replacing an atom of H with the NH_2 group. Nitric acid, HNO_3, must therefore be reduced when its nitrogen is to be employed in the construction of proteid. This reduction is independent both of sunlight and chlorophyll, so that nitric acid can be assimilated in darkness and in colourless parts of the plant. Indirectly, of course, chlorophyll and light are of importance in the synthesis of proteids in so far as compounds containing carbon are required, and these are formed in sunlight with the help of chlorophyll. On account of their rich supply of carbohydrates the foliage leaves are specially fitted for the production of proteid, but they are not "organs of proteid formation" in the same degree as they are organs for the formation of carbohydrates. Only in a few plants (nitrate plants, *e.g. Chenopodium*, *Amarantus*, *Urtica*) can the nitric acid be recognised in the leaves; in most plants it appears to be transformed soon after its absorption by the root.

We know as little of the steps in the assimilation of ammonia as of those of nitric acid. Since no preliminary reduction is required, ammonia might be regarded as more readily assimilable than nitric acid. When ammonia is found to be less favourable in a water culture than nitrates, this may be due to certain subsidiary harmful effects of the former substance.

The hypothetical intermediate products between the nitrogenous compounds absorbed and the completed proteids, *i.e.* various amino-acids and related substances, are present in all parts of the plant. Leucin, tyrosin, and asparagin are especially common. It can, however, rarely be determined whether these substances have been synthesised from ammonia or nitric acid or whether they have arisen by the breaking down of albumen (cf. p. 266).

Nitrogen is present not only in proteids but in LECITHINS and in ORGANIC BASES. The former are complex esters in which glycerine is combined with two molecules of fatty acid, one molecule of phosphoric acid, and the nitrogen-containing base, cholin. They are never absent from living protoplasm. The majority of organic bases (alkaloids) are probably by-products of the assimilation of nitrogen and are not further utilised.

While it can be said that the typical autotrophic plant can assimilate nitrogen as well or better as nitric acid than as ammonia, this does not hold for the majority of Fungi. Only a few of these prefer nitric acid; as a rule ammonia is the best nitrogenous food. Some Fungi lack the power to construct the more complex substances of the plant from such simple nitrogenous compounds, or at least the latter are formed more rapidly and certainly from organic substances. Further, in these Fungi there are various types; some succeed best with amino-acids, others with peptone, while others prefer proteid. They are all heterotrophic as regards their nitrogenous food.

The so-called INSECTIVOROUS or CARNIVOROUS PLANTS must be referred to here ([85]) (cf. p. 185). These are plants provided with arrangements for the capture and retention of small animals, especially insects, and for the subsequent solution, digestion, and absorption of the captured animals by means of enzymes. All these insectivorous plants are provided with chlorophyll; the explanation of their peculiar mode of life can hardly be to obtain organic compounds of carbon. It is further known that they can succeed without animal food, but the moderate supply of an animal substance has a distinctly beneficial effect manifested in increased production of fruits and seeds. It is very probable, though by no means established, that the carnivorous habit is a means of obtaining nitrogen. Whether the nitrogen in the peat or water in which insectivorous plants often grow is insufficient in quantity, or whether its quality is not optimal, must be left undetermined. It is doubtless possible that organically-combined nitrogen is specially advantageous to these plants. This does not exclude the possibility that the insectivorous habit is related not only to the supply of nitrogen, but to that of other nutrient salts, especially of potassium and phosphoric acid. Whether these salts are utilised in organic combinations or are transformed in the digestive process to the inorganic form is unknown. In the latter case the use of the

insectivorous habit would have to be sought in the provision of more nutrient salts than are afforded by the soil.

The insectivorous plants strike the ordinary observer as deviating from ordinary plants in the direction of the animal kingdom. Like animals they utilise solid food which has to be rendered fluid by enzymes before it is absorbed into the cells. The similarity between animals and these plants appears to be increased by a comparison of the stomach and the pitchers, etc., of some insectivorous plants. It should be recognised, however, that some Fungi and Bacteria stand physiologically closer to animals. They can obtain all their food by the digestion of solid organic material, while the insectivorous plants are autotrophic, at least as regards their supply of carbon.

In relation to insectivorous plants certain phanerogamic parasites may be considered which were omitted above (p. 254), since they possess green leaves and are evidently autotrophic as regards their supply of carbon. In spite of this, however, the plants only develop normally, when their root-system is in connection with the roots of other plants by means of disc-shaped haustoria. They may even (as is also the case with *Cuscuta*) enter into this relation with other individuals of the same species. *Thesium*, belonging to the Santalaceae, and the following genera of the Rhinanthaceae, *Rhinanthus*, *Euphrasia Pedicularis*, *Bartsia*, and *Tozzia*, may be mentioned as examples of plants showing these peculiar conditions. In *Tozzia* the parasitism is well marked in the earliest developmental stages. The Mistletoe (*Viscum album*), although strictly parasitic, possesses, like many of the allied foreign genera of the Loranthaceae, fairly large leaves well supplied with chlorophyll, and quite able to provide all the carbohydrates required. By its reduced root-system it obtains, however, from the host plant (as has also been shown to be probable in the case of the Rhinanthaceae ([36])) its supply of water and dissolved salts.

In contrast to these plants, which are either demonstrably or probably supplied with organically-combined nitrogen, there are certain micro-organisms which are strikingly autotrophic as regards nitrogen, while they are heterotrophic as regards their carbon assimilation. These organisms are able to utilise the nitrogen of the atmosphere. Their existence was first established at the end of last century by the work especially of WINOGRADSKI, HELLRIEGEL, and WILFARTH ([37]).

In the first place there are certain Bacteria, such as *Clostridium Pasteurianum* and related forms and *Azotobacter chroococcum*, which live independently in cultivated soil and in water under very various external conditions. They fix free nitrogen and thus possess a very important power both for their own success and for that of many other organisms; this property is of the greatest importance in agriculture. An increasing number of the lower Fungi have been shown by recent researches to have the same power though in less degree. In addition to these free-living forms there are micro-organisms

which occur parasitically in higher plants and have the same property. The best investigated among these are the various forms of *Bacillus radicicola*, which infest the roots of Leguminosae and frequently give rise to enormous numbers of gall-like tubercles upon them (Figs. 251, 252). The Leguminosae thus appear to differ from all other green plants in their

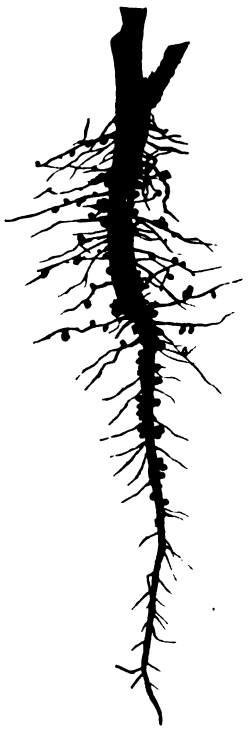


FIG. 251.—A root of *Vicia Faba*, with numerous root-tubercles. (Reduced. After NOLL.)

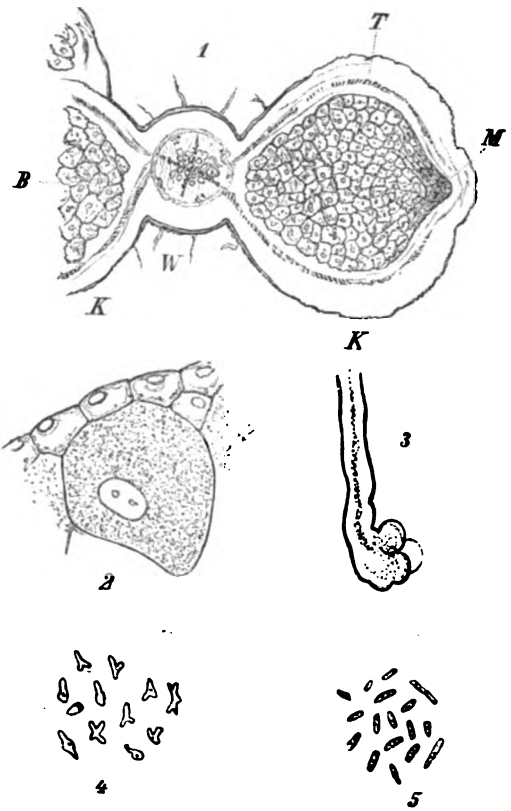


FIG. 252.—*1*, Young tubercles (*K*) on a root (*W*) of *Vicia Faba*, *B*, large-celled tissue filled with masses of Bacteria, *M*, the "meristem" of this. *T*, tracheides. (× 60.) *2*, A cell of the tubercle filled with thousands of Bacteria, and beside it some un-infected cells. (× 320.) *3*, An infected root-hair containing the "infection hypha." (× 320.) *4*, Bacteroids. *5*, Unaltered Bacteria. (× 1200. After NOLL.)

mode of accumulating nitrogen (38); this was first established by GILBERT and LAWES in England and SCHULTZ-LUPITZ in Germany.

The rod-shaped bacteria penetrate through the root-hairs into the cortex of the roots, and there give rise to the tubercles. These tubercles become filled with a bacterial mass, consisting principally of swollen and abnormally-developed (hypertrophied) BACTERIOIDS, but in part also of bacteria, which have remained in their normal condition. While the bacteria live on carbohydrates and at first

also on albuminous substances supplied by the host plant, the latter profits by the power of fixing free nitrogen possessed by the bacterioids. The bacterioids furnish a steady supply of combined nitrogenous substance to the leguminous plant. It has been calculated that Lupins are able in this way to obtain 200 kg. of nitrogen per hectare. The agricultural importance of this natural fixation of nitrogen will be evident. It has been attempted to further it by infecting fields with soil rich in the bacteria, or with pure cultures of specially active forms ("nitragin"). A marked increase in the crop of *Serradella* is obtained in this way. If the soil in which a Leguminous plant is grown contains a sufficiency of nitrates, the plants may live at their expense; since the presence of nitrates exerts an injurious influence on *Bacillus radicicola*, practically no nodules are formed under such circumstances.

Besides the Leguminosae, *Elaeagnus* and *Alnus* are able to utilise free atmospheric nitrogen when their roots bear nodules; these are due to infection by another of the lower organisms. A species of *Podocarpus* which has a mycorrhiza can also utilise atmospheric nitrogen. It is thus not improbable, though as yet unproved, that other mycorrhizas may have a similar significance. The roots not only of the phanerogamic plants without chlorophyll, referred to on p. 256, but also of most green plants living in the humus soil of woods and heaths, especially the trees, stand in close relation to Fungi [39].

The fungal hyphae are sometimes found within the root occurring in tangled groups in the cells of definite cortical layers, while individual filaments extend into the soil. In other plants the hyphae invest the outer surface of the young roots with a closely-woven sheath. The former is called endotrophic, the latter ectotrophic mycorrhiza, but the extreme forms are connected by intermediate conditions. The fungi of the endotrophic mycorrhiza are in part digested by the cells of the root, and thus all the substances liberated will be available for the phanerogamic plant. This is not known in the case of ectotrophic mycorrhiza. STAHL regards the significance of fungal infection of the flowering plant to lie in the active absorption of nutritive salts from the soil by the fungus. The advantage to the fungus is obviously, at least in the cases in which it infects green plants, the provision of carbohydrates which it obtains. It is probable that the consortia of Fungi and Algae which are called Lichens can be ranked here as regards their physiology of nutrition [39a].

More recently swellings which are due to infection by bacteria have been discovered in the leaves of tropical plants belonging to the Rubiaceae and Myrsinaceae. While, however, in the case of the Leguminosae the infection always depends on accidental meeting of the bacteria and the flowering plant, in these families the bacteria are present in the embryo of the plant. When they are artificially kept from the egg-cell the development of *Ardisia* is abnormal. It is quite probable that in these cases also an assimilation of free nitrogen takes place [40].

C. ASSIMILATION OF OTHER SUBSTANCES

Sulphuric acid most nearly resembles nitrogen since it also is used in the construction of proteids which contain about $\frac{1}{2}$–$1\frac{1}{2}$ per cent of S. It is still uncertain where and under what conditions its assimilation occurs; we only know that a reduction of acid radicals must take place in the process. In some plants sulphur is combined in other substances besides proteids.

Phosphoric acid is connected with sulphuric acid in so far as it is employed in the construction of at least some proteid substances, especially the nucleo-protein of the cell nuclei; it forms from 0·3 to 3 per cent of this. In entering into the molecule of this substance the phosphoric acid, unlike sulphuric acid, is not reduced. Lecithin (cf. p. 258), which is present in all plants, also contains phosphorus, and this is also the case for phytin, which occurs especially in seeds.

The Metals.—As may be shown by the method of water culture, potassium, calcium, magnesium, and iron are just as essential as any of the substances hitherto mentioned. It is very probable, at least for potassium and magnesium, that they take part in the construction of certain compounds that are essential for the existence of the plant. Probably protoplasm contains these elements. Other substances also may contain them; thus, for instance, a considerable amount of magnesium has been shown to exist in chlorophyll. It was formerly believed that chlorophyll contained iron because the chloroplasts remained yellow when iron was omitted from the food solution. It is now known that chlorophyll does not contain iron and that iron is also necessary for plants that are not green. This supports the assumption that protoplasm itself contains iron, and that the "chlorosis" which occurs when iron is wanting is a result of a diseased condition of the protoplasm.

Since potassium, magnesium, and iron thus pass into the substance of the plant they must be assimilated, but we know nothing of how or where this happens. The case of calcium is somewhat different; it is not invariably essential, for some Algae can succeed without it. In other plants it has a protective function, preventing the poisonous effects which result from iron, magnesium, potassium, and sodium, and also from phosphoric acid, sulphuric acid, nitric acid, and hydrochloric acid. It is, however, improbable that the indispensability of calcium in the case of the higher plants is merely due to this protective function.

In speaking of insectivorous plants and of certain green parasites it was mentioned that they might perhaps obtain their mineral food-materials in organic compounds; nothing certain is known on this point.

Water.—We know that water is essential to the plant. When it is taken into the plant as water without undergoing chemical change we do not speak of its "assimilation." This is the case, for example, in the water which fills the vacuoles of cells or that which permeates the protoplasm and cell wall. It is different where the water is chemically combined. This necessarily takes place when carbohydrates are formed from carbon dioxide, and probably in other cases also. In these cases there is the same justification for speaking of the assimilation of the water as of the assimilation of carbon dioxide.

IV. Translocation and Transformation of Assimilates

The assimilates serve primarily for the construction of new substance of the plant and the growth of new cells. They are also employed as reserve materials and as substances in course of translocation, while some are used up in the metabolism and others in the production of excretions and secretions.

It is only rarely, however, that growth takes place where the work of assimilation is effected. Thus the assimilation of carbon dioxide goes on mainly in fully-grown foliage leaves while the growing points are more or less distant from the leaves. The assimilatory activity and the formation of new organs also do not coincide in time. Many plants have periods of active assimilation when but little growth is taking place and, alternating with these, periods of active growth associated with little or no assimilatory activity. Our trees lose their leaves in autumn and herbaceous plants lose all the above-ground organs. In both cases new organs of assimilation must be formed in spring before assimilation can be resumed; in the growth of these organs the plant utilises stored assimilates. Every germinating seedling also lives at first wholly at the expense of assimilates of a preceding generation. Such stored-up assimilates are termed RESERVE MATERIALS; they may be deposited where they are formed or may be carried to secondary places of deposit. Every foliage leaf which in the evening of a bright summer's day is gorged with starch is an illustration of the first condition. The second is seen in seeds where reserve materials are stored in the endosperm or the cotyledons. It is also found in vegetative organs, which may even show by their form that they are places for storage of reserve materials; examples of these are the swollen leaves of bulbs, swollen stems (*e.g.* potato), or swollen roots (*e.g.* turnip). In order that assimilates should reach these storage places they must be capable of TRANSLOCATION, and they have also to be conveyed through the plant when they are removed from the place of storage and employed in the development of new organs. Many reserve materials or assimilates occur in a solid form which does not allow them to pass from cell to cell; starch is an example of this. Others are, it is true, soluble, but have such large molecules that they only diffuse with difficulty. For these reasons reserve substances have usually to undergo a change before they can be conveyed through the plant.

A. MOBILISATION OF RESERVE MATERIALS

In the mobilisation of reserve materials we have usually a not very profound change of the nature of a hydrolysis, *i.e.* a splitting of the substance into smaller molecules with the absorption of water.

This must be separately considered for the three main types of reserve material, the carbohydrates, the fats, and the albuminous substances.

1. Hydrolysis of Carbohydrates

Starch is one of the most important reserve materials in plants. It not infrequently forms the main part of the reserve substance in seeds as well as in tubers and bulbs. In the potato tuber 25 per cent and in the grain of wheat 75 per cent of the fresh weight consists of starch. It is also present in considerable amounts in the pith, the xylem parenchyma, the medullary rays, and the rind of trees. The starch has to be broken down in order to allow of its translocation. This is effected technically by treatment with acids; the grape-sugar of commerce is obtained by treating potato-starch with sulphuric acid. The molecule of starch is split up into numerous molecules of dextrose according to the formula

$$(C_6H_{10}O_5)_n + nH_2O = nC_6H_{12}O_6.$$

In the plant this hydrolysis is effected not by means of acids but by a special organic substance called diastase. Diastase can be extracted from the organs by water or glycerine, precipitated by means of alcohol from the extract and again dissolved, without any essential change in its properties. On the other hand, diastase is very susceptible to high temperatures, and is rendered permanently inactive by heating to about 75° C. It has not yet proved possible to obtain chemically pure diastase; it is always mixed with proteids and was therefore for long regarded as of this nature. Remarkable views which have more recently been formed as to its chemical nature and its formation still require confirmation ([40a]).

Diastase has the same effect on starch as sulphuric acid has; they both act as catalysators. The name catalysators is given to substances which influence the rapidity of a chemical reaction. We are mainly concerned with the aeceleration of reactions. The usual method in the chemical laboratory of accelerating a reaction is the application of heat; the fact that the life of the organism is confined to a narrow range of temperature limits this method. A second method is by the use of inorganic catalysators. Many of these, such as sulphuric acid mentioned above, injure the protoplasm; it is thus easy to understand why the organism should form special catalysators that are not injurious. These are termed ENZYMES ([41]) and occur in both plants and animals. While many inorganic catalysators influence very various chemical processes, the influence of organic catalysators is quite specific; thus diastase only acts on starch. Since the catalysator either does not enter into the reaction or at least does not do so permanently, a small amount of it is able to hydrolyse a large

quantity of the substance acted on, if the products of the reaction are continually removed.

Diastase is found in many parts of the plant, especially in those which contain much starch, such as foliage leaves and germinating seeds. The amount of diastase in an organ is not constant, but is regulated according to the needs of the plant; further, its action can be arrested by the formation of other enzymes (anti-enzymes). This is one of the many regulatory processes so characteristic of the organism.

In the plant diastase acts on the starch grains. These are corroded under its influence; they are dissolved away from without inwards, but this proceeds as a rule irregularly, so that the shape of the grain changes. At particular spots the diastase eats more quickly into the grain and, using pre-existing splits and canals, breaks it up into smaller portions which then dissolve further (Fig. 253). Outside the plant the action of diastase can best be shown on thin starch paste; on adding diastase to this the characteristic iodine reaction is lost after a few minutes or a quarter of an hour. The blue colour given at first, changes to a wine-red tint, and ultimately a yellow colour is given. Dextrin is an intermediate product between the starch and the maltose.

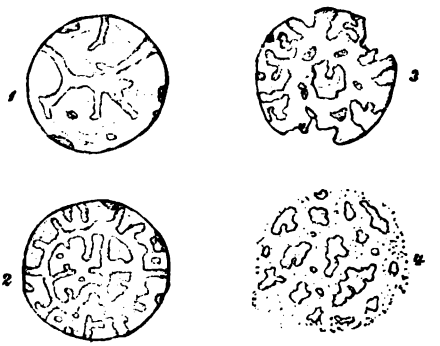


FIG. 253.—Different stages of the corrosion shown by the starch grains of germinating Barley. (After NOLL.)

Cellulose is also of frequent occurrence as a reserve substance. In the endosperm of many seeds the cell walls are very strongly thickened and the thickening layers are dissolved in the process of germination. Such thickened walls are beautifully shown in many palm seeds, *e.g.* in the Vegetable Ivory Palm. The solution of the thickening is due to an enzyme, the so-called cytase, which, however, does not act on every variety of cellulose. Typical cellulose (p. 38) is not attacked by it, but only reserve cellulose, which differs in its chemical structure.

Inulin, which is found especially in Compositae and Campanulaceae, is related according to its empirical formula $(C_6H_{10}O_5)_n$ with cellulose and starch, but is distinguished from these substances by always occurring in plants in the dissolved form. In spite of this it is incapable of translocation on account of the size of its molecule, and is broken down on germination by an enzyme into a sugar of the formula $C_6H_{12}O_6$. The sugar in this case is, however, levulose.

Cane Sugar, which occurs for example in the sugar-cane and sugar-

beet, may be connected with inulin. It is converted by the widely-spread enzyme "invertin" into equal parts of dextrose and levulose.

2. The Fats

Though we are unable to manufacture the reserve carbohydrates mentioned either from dextrose or levulose, we can understand that it is as easy for the plant to build them up as to break them down. It is much more difficult to understand in what way the plant is able to form fats (glycerine esters of various fatty acids; cf. p. 30) from carbohydrates. Fats are always present in living protoplasm; the general distribution of lecithin which is derived from fats has already been mentioned. Fats occur in relatively large amounts as reserve materials, but not in the assimilating foliage leaves. They occur in large amount in many ripe seeds, where they are formed at the expense of carbohydrates. At germination they are decomposed by the enzyme lipase into fatty acids and glycerine. The fatty acid is capable of passing through the water-saturated cell wall more readily than the fat, but does not usually travel as such for any considerable distance in the plant; it is usually quickly converted into a carbohydrate. A fatty oil sometimes occurs in the succulent portions of fruits, *e.g.* in the oil-palm and the olive, and then does not enter again into the metabolism of the plant.

3. Albuminous Substances

Albumen occurs in the storage places for reserve materials partly in a crystalline and partly in an amorphous form. The crystals occur free in the cytoplasm, nucleus, or in the chromatophores; in seeds they are found especially in the aleurone grains, where they are associated with globoids. The latter then contain Ca, Mg, and phosphoric acid in an organic compound (cf. p. 31).

The products of the hydrolytic breaking down of albuminous substances are mainly amino-acids, the wide distribution of which in the plant has already been referred to. When seeds rich in proteid such as *Ricinus*, *Pinus*, etc., are germinating, the abundant amino-acids may be regarded as derived from the proteid. Amino-acids occurring in other situations may have arisen in the synthesis of proteids. The proteid-molecule does not produce at once or exclusively amino-acids; the breaking down of the very large molecule is a gradual one, in which the bodies which appear first have many properties in common with proteids; first comes albumose, then peptone, and only then amino-acids. With the latter appear ammonia, also products of decomposition containing sulphur and phosphorus, and generally carbohydrates also.

This hydrolytic breaking down of proteids takes place under the influence of "proteolytic" enzymes (proteases) which very probably are closely similar to corresponding enzymes in the animal body. We should therefore have to distinguish

1. Pepsin, which only breaks down the proteid molecule to albumoses and peptone.

2. Erepsin, which transforms peptone into amino-acids. It is uncertain whether in addition there should be added

3. Trypsin, which transforms proteids directly into amino-acids.

The decomposition products of albumen quickly undergo changes in the plant, and therefore the mixture of nitrogenous organic compounds which one obtains from a plant kept in the dark is not identical with the products of the hydrolysis of albumen outside the plant. In the plant syntheses take place after the primary decomposition, and these lead to the formation of such substances as amides, the most widely spread of which is asparagin. This dominates in Gramineae and Leguminosae (15 g. are present in a litre of sap from bean seedlings); it is replaced in Cruciferae and Cucurbitaceae by glutamin, while in the Coniferae arginin, a di-amino-acid, appears to play the same part. The syntheses proceed still farther in light, when proteid may again be formed from the products of decomposition of albumen.

B. Transport of the Mobilised Reserve Materials

When the reserve materials have been brought by the aid of the proper enzymes into the soluble form, or have been transformed into substances with smaller molecules, they are capable of being transported; we may speak of them as being mobilised. Their movements are governed by the general principles of translocation of substances. It is especially necessary that a diffusion current should be established and maintained. This is brought about by the active growth of cells at a greater or less distance from the place of storage of the reserve material. As long as this lasts each molecule on its arrival at the place of growth is promptly transformed (*e.g.* sugar into starch or cellulose), and thus room is made for the molecules that follow. In non-growing organs also (*e.g.* cotyledons, endosperm) a gradient of diffusion is established by the cells to which the current passes, having a greater power of condensing the sugar (forming starch) than the others. A diffusion current can also be artificially established where a storage structure under proper conditions is placed in relation on one side with a large amount of water. It is thus possible to bring about artificially an emptying of seeds, bulbs, etc.

When substances have to be transported for considerable distances, the movement of diffusion, since it goes on slowly, is replaced by movement in mass. Thus in spring the reserve materials deposited in the wood of our trees are carried up by the ascending current of water in these vessels; at this season the fluid in the vessels contains

abundant glucose. In the other direction a stream of mobilised reserve material can pass downwards from the foliage leaves by way of the sieve-tubes ([42]). While, however, the mechanical causes of the transpiration stream are at least partially understood, so far as they depend upon the evaporation of water, we do not know the forces concerned in movements in mass in the sieve-tubes.

Another example of translocation is afforded by leaves shortly before they are shed. In many but not all cases the useful materials in the leaf are transferred to the stem and thus are not lost to the plant. Phosphoric acid, potassium, and nitrogenous substances are thus transferred to the stem, but the cell walls, a protoplasmic layer, and osmotically-active substances in the vacuole remain so that the leaf falls in a turgescent condition ([43]).

C. Further Metamorphoses of Substance

Regeneration of Reserve Materials.—Sooner or later the reserve materials mobilised by the help of enzymes are again converted into substances with large molecules. This occurs at any rate at the end of their transport, whether they are again deposited as reserve materials or are employed as constructive substances. Thus, for example, glucose formed in a leaf may pass to a seed or a tuber and be there transformed into starch or cell wall. When the transport is for a considerable distance the formation of reserve material may go on by the way and not only at the end of the journey. This is specially well seen in the case of starch. Along the routes of sugar transport so-called transitory starch may be formed in every cell. This starch formation diminishes the concentration of the solution, and thus helps to maintain the continued motion of the diffusion current.

Other Products of Metabolism ([44]).—Only a small proportion of the substances met with in plants have been enumerated above. It will be sufficient to mention here the organic acids, tannins, glucosides, alkaloids, colouring matters, ethereal oils, resins, gum-resins, caoutchouc and gutta-percha among the legion of substances which are derived from the products of assimilation. The organic acids will be referred to later (p. 271); the origin and physiological significance of the others are too little known for them to be dealt with. It is known that as a rule they are not further utilised after their formation. They are probably, therefore, by-products of the metabolism of the plant. They need not, however, for this reason be useless, and it is believed that some bitter or poisonous substances protect the plant from being eaten by animals; some pigments are of use in the attraction of animals which distribute pollen, seeds, and fruits, or frighten away injurious animals (warning colours). Resin and latex when they exude and harden may assist in the closing of wounds.

The Ripening of Succulent Fruits.—A striking transformation of substances takes place in the ripening of succulent fruits. The relatively rare case of the formation of fats has already been mentioned. Much more frequent is the change of starch into sugar associated with the disappearance of organic acids and tannins. The fruits thus become sweet-tasted instead of acid or bitter, and are eaten by animals which distribute the seeds. The significance of these chemical changes is thus ecological.

V. Respiration and Fermentation

In the higher plants all the organic substance produced in assimilation is not used for construction and storage purposes; a part of it is always broken down and returns to the state of inorganic compounds. The significance of this process, which is usually associated with the absorption of oxygen and is termed respiration, does not lie in the substances formed but in the liberation of energy which is essential for the life of the plant. In certain lower plants the necessary supply of energy may be obtained in other ways. Usually organic substances are absorbed from the substratum and broken down without being first assimilated. The decomposition may be effected by oxidation, reduction, or dissociation; all these processes are grouped together as fermentation. Other lower organisms can utilise the energy set free in the oxidation of certain inorganic compounds. Transitional forms occur between the various methods of obtaining the necessary energy.

A. Respiration

By respiration in its typical form is understood the oxidation of organic material to carbon dioxide and water; this involves the absorption of oxygen from without (cf. p. 244).

In the higher animals the process of respiration is so evident as not easily to escape notice, but the fact that plants breathe is not at once so apparent. Just as the method of the nutrition of green plants was only discovered by experiment, so it also required carefully-conducted experimental investigation to demonstrate that PLANTS ALSO MUST BREATHE IN ORDER TO LIVE; that, like animals, they take up oxygen and give off carbonic acid. The question had already been thoroughly investigated by SAUSSURE, and by DUTROCHET in the years 1822 to 1837, and its essential features correctly interpreted. Later the existence of respiration in plants was doubted owing to the demonstration of their power of decomposing carbon dioxide and giving off oxygen; it seemed impossible that both processes could go on at the same time. The correct view was then formulated by SACHS. ASSIMILATION AND RESPIRATION ARE TWO DISTINCT VITAL PROCESSES CARRIED ON INDEPENDENTLY BY PLANTS. WHILE IN THE PROCESS OF ASSIMILATION GREEN PLANTS ALONE, AND ONLY IN THE

LIGHT, DECOMPOSE CARBONIC ACID AND GIVE OFF OXYGEN, ALL PLANT ORGANS WITHOUT EXCEPTION BOTH BY DAY AND BY NIGHT TAKE UP OXYGEN AND GIVE OFF CARBONIC ACID. Organic substance, obtained by assimilation, is in turn lost by respiration. That green plants growing in the light accumulate a considerable surplus of organic substance is due to the fact that the daily production of material by the assimilatory activity of the green portions is greater than the constant loss which is caused by the respiration of all the organs. Thus, according to BOUSSINGAULT'S estimates, in the course of one hour's assimilation a plant of Sweet Bay will produce material sufficient to cover thirty hours' respiration. If assimilation is suppressed by keeping the plant in darkness, it loses considerably in dry weight.

Plants produce in twenty-four hours about five to ten times their own volume of carbonic acid. In shade plants this is usually reduced to twice the plant's volume, while the commonly-cultivated *Aspidistra* produces only one-half of its own volume, and can therefore succeed even under conditions which are unfavourable to assimilation.

In order to demonstrate the existence of respiration either the absorption of oxygen or the giving off of carbon dioxide by the plant may be employed. If a handful of soaked seeds is placed at the bottom of a glass cylinder, the top of which is closed for a day by a glass plate, the oxygen in the space is used up by the germinating seeds; a candle will be extinguished if it is introduced into the cylinder. If germinating seeds or flower-heads of Compositae (B, Fig. 254) or young mushrooms are placed in a flask and prevented from falling out when the flask is inverted by means of a plug of cotton-wool (W), the mouth of the flask can be dipped under mercury (S) and some solution of caustic potash (K) be introduced above this. The carbon dioxide formed is then absorbed by the caustic potash and the mercury rises (Fig. 254). When this experiment is carried out quantitatively it is found that a fifth of the volume of air disappears, so that all the oxygen has been absorbed. Since, however, when no potash is present, the volume of gas is not altered by the respiration of the plants, an equal volume of carbon dioxide must be formed for each volume of oxygen that is absorbed. The respiratory coefficient or ratio between the absorbed oxygen and the excreted carbon dioxide is equal to unity $\left(\frac{CO_2}{O_2} = 1\right)$. If we assume that sugar is the substance respired, this must take place according to the formula

$$C_6H_{12}O_6 + 6O_2 = 6CO_2 + 6H_2O.$$

This is an exactly opposite process to the assimilation of carbon dioxide. It is not so easy to demonstrate the formation of water in typical respiration as it is to show the utilisation of oxygen and the production of carbon dioxide. Quantitative estimates of the loss of dry

weight and of the carbon dioxide formed show that the latter does not account completely for the former; a part of the dry substance must thus have been transformed into water.

The volume of air does not under all circumstances remain unchanged by the respiration of the plant; the carbon dioxide produced is not always equal in volume to the oxygen which disappears. Small deviations from this ratio occur in all plants, and considerable ones in, for instance, the germination of fatty seeds, and in the leaves of certain succulent plants (Crassulaceae). This is connected with the fact that in these seeds fats, which are much poorer in oxygen than carbohydrates, are used in respiration; and that in the Crassulaceae certain organic acids are produced from carbohydrates instead of carbon dioxide and water. In other plants also similar acids, though not in so great amount, are formed. They probably arise mainly in the respiratory process, but may also be produced in constructive metabolism.

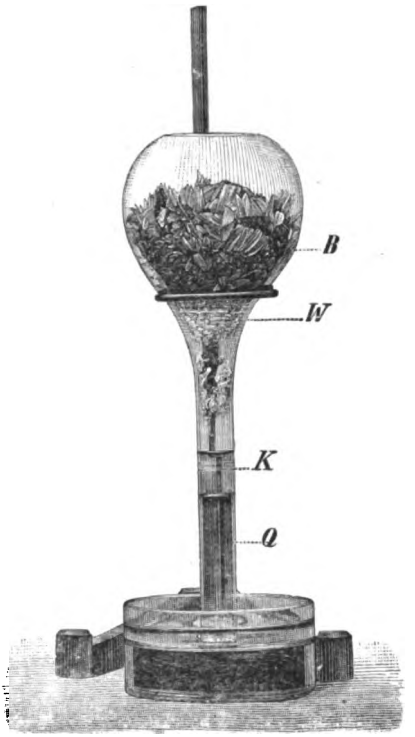


FIG. 254. — Experiment to demonstrate respiration. The inverted flask (*B*) is partially filled with flowers which are held in place by the plug of cotton (*W*). Owing to the absorption of the carbon dioxide exhaled in respiration by the solution of caustic potash (*K*), the mercury (*Q*) rises in the neck of the flask. (After NOLL.)

In the germination of fatty seeds far more oxygen is absorbed than carbon dioxide is given off; this may go so far that in the first days in the dark, in spite of continual respiration, an increase in the dry weight takes place. The respiratory quotient is thus less than 1. Most of the oxygen is used in the transformation of fats, which are poor in oxygen, into carbohydrates, and only a small proportion is used in respiration.

In the Crassulaceae a large proportion of the carbohydrate is changed into organic acids in the process of respiration. The oxidation is thus incomplete; it does not lead to the formation of CO_2, so that less of this gas is formed than the amount of oxygen absorbed would lead us to expect. The respiratory quotient is less than 1. This peculiar respiratory process which is connected with an accumulation of acids in the cell sap, as can be recognised by the taste, is not without ecological significance for succulent plants. The acids formed (especially malic and oxalic acids) give off CO_2 in the light. This can be again employed in assimilation,

while, in typical respiration at least, the CO_2 formed during the night escapes, and is lost to the plant. The succulents thus economise their supply of C, which is probably connected with the fact that they do not so readily obtain carbon dioxide from the air as other plants, owing to the diminution of gaseous exchange on account of the limitation of transpiration.

As has been mentioned, respiration is of general occurrence in the higher plants. It not only occurs in the parts of plants which do not possess chlorophyll and are commonly used in experiments on respiration, but can be demonstrated also in cells which contain chlorophyll. In this case the respiration in the light is masked by the quantitatively greater process of assimilation; it appears only as a diminution in the products of assimilation. If the light is diminished assimilation ultimately ceases and the respiration becomes evident.

Though respiration goes on in every cell its intensity varies greatly in different organs and under various external conditions. Actively-growing parts of plants, young fungi, germinating seeds, flower-buds, and especially the inflorescences of Araceae and Palms, exhibit very active respiration. In some Bacteria and Fungi this exceeds, as compared with the body-weight, the respiration of the human body. In most cases, however, especially in parts of plants composed wholly or mainly of full-grown tissues, the consumption of oxygen and production of carbon dioxide is considerably less than in warm-blooded animals. Among external conditions which have an important influence on the intensity of respiration the temperature and the amount of oxygen must be especially mentioned. An increase of temperature accelerates respiration as it does all the vital processes. The production of carbon dioxide is about doubled or trebled by a rise of 10° C., just as other chemical processes outside the plant are. With continued rise of temperature, however, the respiration diminishes. In contrast to other like phenomena the fall in the respiratory curve is exceedingly steep, so that the optimum and maximum almost coincide.

Respiration is commonly spoken of as a process of combustion. Were this correct it might be expected that the amount of available oxygen would be of fundamental importance; in particular it might be anticipated that respiration would be greatly increased in pure oxygen and completely suspended in a space free from oxygen. Neither of these assumptions is true. Respiration is not markedly increased in pure oxygen, and only at a pressure of 2-3 atmospheres of oxygen does an increase in the respiration become perceptible; this is soon succeeded by a decrease in the respiration indicating the approach of death. Even more striking is the fact that plants in the absence of oxygen continue to produce carbon dioxide. In this case one cannot speak of a process of combustion; the phenomenon is termed INTRAMOLECULAR RESPIRATION ([45]) because the carbon dioxide which is formed owes its origin to a rearrangement of the atoms in the molecule

of the sugar which serves as the material for respiration. The molecule of sugar breaks down and forms, in addition to carbon dioxide, other reduced compounds. Sometimes, for example, alcohol according to the formula

$$C_6H_{12}O_6 = 2C_2H_6O + 2CO_2.$$

If this empirical formula is replaced by the structural formula

$$\begin{aligned} &COH.CHOH.CHOH.CHOH.CHOH.CH_2OH \\ &= CO_2 + CH_3.CH_2OH + CH_3CH_2OH + CO_2, \end{aligned}$$

it will be seen that the molecule of sugar has broken down into four portions, two of which are poorer and two richer in oxygen than the molecular groups from which they are derived. In this type of respiration certain molecular groups withdraw the combined oxygen from others.

It may be assumed that oxygen-respiration and intramolecular respiration are expressions of one and the same property of the plant; in other words, that on withdrawal of oxygen normal respiration passes over into intramolecular respiration. If this is true, it follows that the essence of respiration does not consist in an oxidation process but in a breaking down of organic substance in which products arise that readily take up oxygen. The materials which are respired in the plant, such as carbohydrates and proteid, are not easily oxidisable at ordinary temperatures. Fats, it is true, which may also serve as material for respiration, are oxidisable, but in this case we know that they are transformed into carbohydrates before they are used for respiration by the plant. The plant must thus have at its disposal special means in order to carry on the oxidation and the preceding decompositions that are involved in respiration. It is scarcely to be doubted that enzymes are concerned in this, but we have at present no insight into their precise action (46).

At first sight respiration appears a contradictory process, since in it organic material which has been built up in assimilation is again broken down. Its meaning only becomes evident when, turning from the changes of substance, those of energy are considered. It is not the production of CO_2 and H_2O that is important, but only the liberation of energy. This is effected on the breaking down of such substances as carbohydrates, for the construction of which, as has been seen, a supply of energy is requisite. On this liberated energy the plant is dependent for the driving force in many of its vital phenomena. Movement of protoplasm, growth, and movements due to stimuli cease on the withdrawal of oxygen from the plant. All these vital phenomena begin again on the restoration of a supply of oxygen, if this is not too long delayed. It might have been expected that the organism would possess arrangements by the help of which the external energy of light or heat could be employed

as driving power. Practically, however, it is found that the plant proceeds to store up the energy of the sun's rays in the form of potential chemical energy, and then utilises this at need.

In intramolecular respiration also energy is set free; this does not, however, suffice in most organisms to maintain the driving force for the vital processes. Some seeds can remain alive for many hours or days with intramolecular respiration, and some even continue to give off the same amount of carbon dioxide as in ordinary respiration. In most cases, however, the amount of CO_2 rapidly diminishes. In other plants death soon occurs, probably owing to the reduced compounds acting as poisons. The value of intramolecular respiration is in these cases only slight. On the other hand it has a very great importance in certain organisms which will be referred to later.

B. Oxidation of Inorganic Material (47)

While most plants use organic compounds, especially carbohydrates, in respiration, certain Bacteria utilise other sources of energy. Thus, the nitrite bacteria which commonly occur in the soil oxidise ammonia to nitrous acid, and the associated nitrate bacteria further oxidise the nitrous acid to nitric acid. By the help of the energy thus obtained they can then—as has already been pointed out on p. 254—assimilate carbon dioxide; the chemical energy takes the place in them of the sun's energy for the typical autotrophic plant. There is no breaking down of organic material so that the whole of the assimilated nutritive substance is retained, and the working of these organisms is very economical. Since, however, only a limited amount of ammonia is available, and this is derived from other organisms, they cannot take the dominant place in nature which the green plants do.

With the nitro bacteria the so-called sulphur bacteria may be associated; these oxidise sulphuretted hydrogen to sulphuric acid, sulphur being an intermediate product, and being stored in the body of the plant. In the same way as the sulphur bacteria utilise the energy set free in the oxidation of sulphuretted hydrogen, the iron bacteria obtain usable energy by the oxidation of ferrous to ferric oxide, other bacteria by the oxidation of methane to carbon dioxide and water, and yet others by that of hydrogen to water.

C. Fermentation (48)

With the removal of oxygen intramolecular respiration begins, but this cannot supply the necessary energy to maintain life in the higher plants, although it may do so in lower organisms. Many Bacteria, Fungi, and certain Algae (Characeae) are notably independent of a supply of oxygen; they succeed with slight traces of this gas, or they avoid it altogether and live in situations where oxygen is absent.

Such organisms are called anaerobes or anaerobionts in contrast to the typical aerobes or aerobionts. All intermediate stages connect the two extremes. The true anaerobionts decompose large amounts of organic substances, and this decomposition, which is in principle the same as the process of intramolecular respiration, is termed FERMENTATION. As in intramolecular respiration, these processes are concerned with obtaining combined oxygen.

The prototype of fermentation is the alcoholic fermentation brought about by the yeast fungus. In this sugar is split up into alcohol and carbon dioxide, and the process has great technical importance in the production of beer, wine, and brandy. The chemical process is the same as that of intramolecular respiration in a green plant; in contrast to this the yeast plant obtains in the fermentation a complete substitute for respiratory activity. It is, however, only independent of oxygen when it is supplied with a suitable fermentable material (sugar). In the absence of sugar, oxygen is indispensable, and normal respiration takes place. When both sugar and oxygen are supplied, respiration and fermentation go on simultaneously; part of the sugar is transformed into C_2H_6O and CO_2 and another part into H_2O and CO_2. Obviously, the transformation of sugar into alcohol and carbon dioxide will provide much less energy than the complete combustion to carbon dioxide and water. It is thus easy to understand that yeast utilises enormous quantities of sugar. Only about 2 per cent of the sugar in the nutrient solution is used in the construction of the substance of the plant, *i.e.* is assimilated; the rest is fermented. For effecting this extensive decomposition of the sugar, yeast employs a specific enzyme (zymase), the existence of which was demonstrated by E. BUCHNER ([49]).

Many other carbohydrates undergo fermentations, and this also holds for proteids. In the latter case the process is termed putrefaction when it takes place in the absence of oxygen, and decay when oxidation is possible. In nature aerobic bacteria occur first in the fermentation of albuminous substances, and these prepare the way for anaerobic forms, so that a sharp distinction between decay and putrefaction is impossible. In all cases the proteids are first hydrolytically dissociated with the production of the substances already mentioned, especially amino-acids. These are further changed, first by the separation of NH_2, and then more profoundly; ill-smelling substances such as indol and skatol are often, but not in all cases of proteid fermentation, formed. It is impossible to draw a sharp line between those decompositions which go on without the assistance of atmospheric oxygen and those in which oxygen plays a part. We are obliged to class as fermentations all those metabolic processes by which energy is obtained, which differ from typical oxygen respiration. In this sense the oxidation of alcohol to acetic acid effected by the acetic acid bacteria and also the production of acids in the higher plants, especially in succulent

plants (p. 271), would be fermentations. Lastly, the processes of denitrification and of reduction of sulphates, in which anaerobic bacteria—probably in order to obtain oxygen—reduce nitrates to free nitrogen and sulphates to sulphuretted hydrogen, cannot be excluded from fermentations.

Many fermentations have another significance besides that of obtaining energy. The products of fermentation such as alcohol, acids, etc., are poisons; they are, as a rule, more injurious to other organisms than they are to those which produce them. On this account they are suited to exclude other organisms from the supply of food-material. It is true that a fermentation organism in a pure culture on a definite substratum renders, by the products of its metabolism, the latter not only unsuitable to concurrent organisms but sooner or later for itself. When organic material, as is the case in nature with the remains of dead organisms, is the prey of various micro-organisms these co-operate in their action; metabolic products of one kind of micro-organism are further decomposed by others until the organic compounds are converted into inorganic or mineral substances. The final products are water, hydrogen, methane, ammonia, nitrogen, and sulphuretted hydrogen.

Circulation of Material.—All these end-products of fermentation can be utilised by other organisms. Leaving CO_2 and H_2O aside as having been sufficiently dealt with, it may be noted that hydrogen, methane, ammonia, and sulphuretted hydrogen are all oxidised by particular bacteria, while others assimilate nitrogen. It is only by this co-operation of all organisms that life is maintained on the earth and substances again brought into circulation. If only one type of organism existed, it would in a short time have destroyed the possibility of its own existence by its one-sided metabolism.

D. Production of Heat and Light in Respiration and Fermentation

Heat (50).—Since typical respiration is a process of oxidation, it is easy to understand that it is accompanied by an evolution of heat. That this evolution of heat by plants is not perceptible is due to the fact that it is not sufficiently great, and that considerable quantities of heat are rendered latent by transpiration, so that transpiring plants are usually cooler than their environment. In some fermentations, *e.g.* alcoholic fermentation, a considerable quantity of heat is evolved. The heat of rotting manure is well known and employed in the construction of hot-beds.

The spontaneous evolution of heat is easily shown experimentally, if transpiration and the loss of heat by radiation are prevented and vigorously-respiring plants are selected. A quantity of germinating seeds (peas) shows under proper

conditions a rise in temperature of 2° C. The greatest spontaneous evolution of heat manifested by plants has been observed in the inflorescences of the Araceae, in which the temperature was increased by energetic respiration 10°, 15°, and even 20° C. Also in the large flower of the *Victoria regia* temperature variations of 15° C. have been shown to be due to respiration. One gramme of the spadix of an Aroid exhales, in one hour, up to 30 cubic centimetres CO_2; and half of the dry substance (all the reserve sugar and starch) may be consumed in a few hours as the result of such vigorous respiration. These high temperatures in flowers and inflorescences attract insects that are of use in pollination. Specially high temperatures are obtained by cutting up living leaves in large quantity and ensuring a sufficient supply of oxygen. Under these conditions the temperature rises to 40°-50° C., and the leaves perish. After their death a further rise of temperature is due to the action of micro-organisms.

In the healing of wounds in plants, respiration and also the production of heat are markedly increased; the contrary is seen in conditions of starvation.

In the fermentation of tobacco also a considerable rise in temperature takes place. This is still more marked when damp hay or cotton wool is piled up in large quantity and left undisturbed; by the formation of easily inflammable gases, this may lead to the spontaneous combustion of the material. MIEHE has most recently investigated the spontaneous heating of hay. First by the respiratory activity of *Bacillus coli* the temperature is raised to 40° C.; then a number of thermophilous Moulds and Bacteria become established, among which *Bacillus calfactor* raises the temperature to 70° C. Ultimately all the organisms perish owing to the temperature to which they have given rise and the hay becomes sterile.

Phosphorescence [51]. — Under the same conditions as those of respiration a limited number of plants, particularly Fungi and Bacteria, emit a phosphorescent light. The best-known phosphorescent plants are certain forms of Bacteria which occur in the sea, and the mycelium, formerly described as "Rhizomorpha," of the Fungus *Armillaria mellea*. Harmless phosphorescent Bacteria (*Microspira photogena*, *Pseudomonas lucifera*) occur on phosphorescent fish or meat. According to MOLISCH *Bacterium phosphoreum* (*Micrococcus phosphoreus*) usually occurs on meat which has been moistened with a 3 per cent solution of common salt and kept at a low temperature. The most important plants, in addition to many animals, taking part in the phosphorescence seen in the sea are *Pyrocystis noctiluca*, belonging to the Gymnodiniaceae and certain Peridineae.

This phosphorescence at once disappears in an atmosphere devoid of oxygen, only to reappear on the admission of free oxygen. On this account the phosphorescent Bacteria, according to BEYERINCK and MOLISCH, afford a delicate test for the activity of assimilation. All the circumstances which facilitate respiration intensify phosphorescence; the converse of this is also true. According to the results of investigations concerning the phosphorescence of animals, from which that of plants does not probably differ in principle, the phosphorescence is not directly dependent upon the respiratory processes. No use is known for the phenomenon of phosphorescence.

SECTION II

DEVELOPMENT (52)

DEVELOPMENTAL PHYSIOLOGY, which is also spoken of as the MECHANISM OF DEVELOPMENT, will be treated here under three heads. A few introductory remarks will in the first place render more vivid some facts that have already been mentioned in the morphological part. On this follows developmental physiology in the proper sense, the object of which is to understand causally the successive processes in development and to modify these at will. As yet the results obtained do not reach far towards this goal; the problems are more numerous than the solutions. These problems require to be presented from two points of view: in the second sub-section the factors which influence development will be considered, while in the third sub-section the presentation will be based on the developmental processes themselves.

I. Introductory Remarks

Development accompanied by changes of form due to growth is one of the most general and striking of the vital phenomena of the plant. A mere increase in volume does not necessarily imply growth, for no one would say that a dried and shrivelled turnip grows when it swells in water. Only permanent and irreversible increase of size can be termed growth, and this whether the plant as a whole is gaining or losing in substance. Usually growth is associated with gain of material, but in the case of potatoes sprouting in a dark cellar loss takes place by transpiration and respiration, and yet the shoots exhibit growth.

1. The Measurement of Growth.

Total Elongation.—The rate of growth of a plant, or the total elongation in any unit of time, may be directly measured by means of a scale in the case of some quick-growing organs, *e.g.* the inflorescences of *Agave* and the shoots of *Bambusa*. Usually it is necessary to magnify in some way the actual elongation for more convenient observation. This may be effected by means of a microscope, which magnifies the rate of growth correspondingly with the distance grown. For large objects, the most convenient and usual method of determining the rate of growth is by means of an AUXANOMETER.

The principle of all auxanometers, however they may differ in construction, is the same, and is based upon the magnification of the rate of growth by means of a lever with a long and short arm. In Fig. 255, at the left, a simple form of auxano-

meter is shown. The thread fastened to the top of the plant to be observed is passed over the movable pulley (*r*) and held taut by the weight (*g*), which should not be so heavy as to exert any strain on the plant. To the pulley there is attached a slender pointer (*z*), which is twenty times as long as the radius of the pulley, and this indicates on the scale (*S*) the rapidity of the growth magnified twenty-fold.

Self-registering auxanometers are also used, especially in making extended observations. In Fig. 255, at the right, is shown one of simple construction. The radius of the wheel (*R*) corresponds to the long arm, and the radius of the small wheel (*r*) to the short arm of the lever, in the preceding apparatus. Any movement of the wheel, induced by the elongation of the shoot, and the consequent descent of the weight (*g*), is recorded on the revolving drum (*C*) by the pointer attached to the weight *Z*, which is in turn balanced by the counter-weight

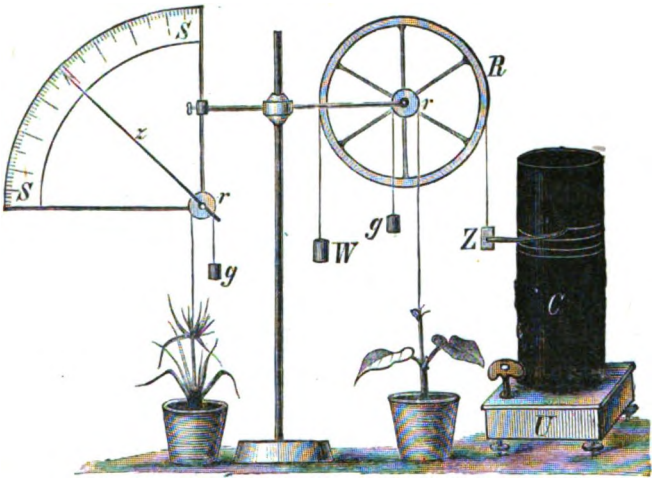


FIG. 255.—Simple and self-registering auxanometers. For description see text.

(*W*). The drum is covered with smoked paper, and kept in rotation by the clockwork (*U*). If the drum is set so that it rotates on its axis once every hour, the perpendicular distances between the tracings on the drum will indicate the proportional hourly growth.

The rate of growth in plants is usually too slow to allow of the result being directly observed after a short time. Only some fungal hyphae and the stamens of some Gramineae grow so rapidly that their elongation is evident, even to the naked eye. The fructification of the Gasteromycetous fungus *Dictyophora* grows in length to the extent of 5 mm. per minute (A. MOLLER), and according to ASKENASY an increase in length of 1·8 mm. a minute has been observed in the stamens of *Triticum* (Wheat). This approximately corresponds to the rate of movement of the minute-hand of a watch. In comparison with these the next most rapidly-growing organ known is the leaf-

sheath of the Banana which shows an elongation of 1·1 mm., and a Bamboo shoot, with an increase in length of 0·75 mm. per minute; a strong shoot of *Cucurbita* grows 0·1 mm. per minute, the hyphae of *Botrytis* grow 0·034 mm., while most other plants, even under favourable circumstances, attain but a small rate of elongation (0·005 mm. and less per minute).

The rate of growth of an organ never remains uniform; even under constant external conditions it gradually increases from very small values to a maximum and then decreases to zero. This phenomenon is known as "the grand period of growth." An example will illustrate its course.

For the first internode of the stem of the Lupine, growing in the dark at a constant temperature, the daily growth observed, measured in tenths of a millimetre, was:

8, 9, 11, 12, 35, 43, 41, 50, 51, 52, **65**, 54, 43, 37, 28, 18, 6, 2, 0.

The grand period is not always so regular as in this example; frequently deviations due to abrupt changes in the growth are apparent.

Distribution of Growth (53).—As a rule any part of a plant is not growing throughout its whole extent but consists of both fully-grown and still growing portions. The latter also are not elongating uniformly but are composed of zones, passing gradually into one another, in which the rates of growth differ. The length and position of the growing zones is not the same in different organs. The growing zone is longer in aerial roots and in extreme cases may amount to 1 m. In roots it is situated at the tip and occupies a length of 5 to 10 mm. The behaviour of stems varies. Those without sharply-defined nodes have a single zone of growth of considerable length (frequently extending to ·5 m.). They thus resemble the aerial roots. In many shoots, especially those divided into nodes and internodes, there are a number of zones of growth separated by fully-grown zones. This is termed intercalary growth and is beautifully shown, for example, in the haulms of grasses, where a growing zone is found at the base of each internode. At the bases of many leaves also, especially of Monocotyledons, an intercalary growing zone is found.

The distribution of growth in any member of the plant is ascertained by periodically measuring the distance between certain natural or artificial marks.

Thus, for example, the tip of the root in Fig. 256 *I* is marked with lines of india-ink at intervals of 1 mm. The marks start from the growing point of the root (0) just behind the root-cap. Twenty-two hours later the marks had been separated from one another as is shown in Fig. 256 *II*. The elongation has been unequal in the different zones; at the upper and lower ends of the marked region it diminishes and thus leads to the fully-grown region on the one hand and the embryonal region at the tip on the other. Between these and nearer to the apical end is a zone where the maximal growth has taken place. If the growth of one transverse zone such as that between 0 and 1 is followed on

successive days it is found that it grows at first slowly, then rapidly, and then again slowly. In other words, every division of the growing zone exhibits the grand period of growth. The millimetre zones marked off from the apex are thus in different stages of their grand periods; the two first are on the ascending side of the curve, 3 and 4 are at the summit, and the others are on the descending slope of the curve. Other organs give corresponding results.

Distinct periods of growth separated by an interval of time occur in the scapes of the Dandelion, the first period in relation to the development of the flowers, the second to that of the fruits. A similar behaviour is found in other organs whose function after a time becomes altered (flower or fruit stalks in *Linaria cymbalaria*, and *Arachis hypogaea*).

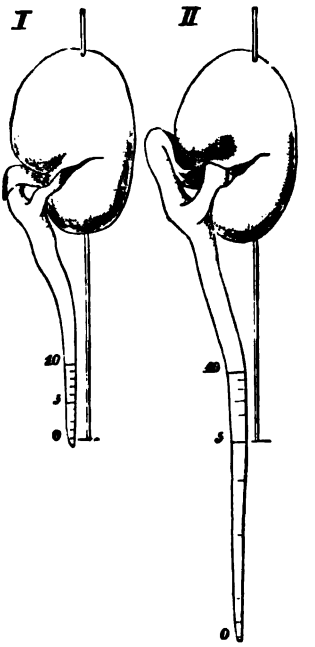


FIG. 256.—Unequal growth of different regions of the root-tip of *Vicia Faba*. *I*, The root-tip divided by marking with india-ink into 10 zones, each 1 mm. long. *II*, The same root after twenty-two hours; by the unequal growth of the different zones the lines have become separated by unequal distances. (After SACHS.)

Rate of Growth.—From the fact that in different organs zones of different length are in a growing condition, it follows that such results as to the total growth of an organ as were described on p. 279 do not give the true rate of growth, *i.e.* the growth of a unit of length in unit time. Thus in the shoots of the Bamboo the growing zone is many centimetres long, while in *Botrytis* it is only 0·02 mm. in length. While *Bambusa* shows twice as much growth per minute as *Botrytis* does, its rate of growth is really much less. To express the rapidity of growth it is necessary to express the elongation per minute as a percentage of the growing zone. This gives a rapidity of growth of 83 per cent in *Botrytis*, and of only 1·27 per cent in *Bambusa*. The maximum growth observed is 220 per cent in some pollen tubes, while some shoots which are still clearly growing have a rate of only 0·5 per cent.

Size of the Plant.—We can only determine the definite elongation of a part of the plant when, in addition to the rate of growth and the length of the growing region, the duration of growth is known. The size of the plant, which, as is well known, depends in various ways on external conditions and yet is a specific character, is determined by variations in these factors. A definite size belongs to the specific properties of an organism just as much as the form of its leaves, etc.; further, the whole organisation of the plant is such that it involves a particular size. The stems of twining plants are particularly long,

while "rosette plants," in which the leaves are separated by hardly recognisable internodes, stand in striking contrast to them.

2. The Phases of Growth

In the simplest plants, such as the lower Algae, Fungi, or Bacteria, development consists merely in growth of the cell followed by cell division. These cases have been sufficiently dealt with in the morphological section. In more complex plants growth and division of cells are also found, but these processes appear subordinated to the growth of the whole. Three distinct processes can be distinguished in this, though they are not always separated in time. These are the stage of FORMATION OF EMBRYONIC ORGANS, that of ELONGATION, and the stage of INTERNAL DEVELOPMENT (54).

(a) Embryonic Rudiments.—The embryonic growth takes place normally at the **growing points**, and new growing points arise as a rule directly from the latter. Only in the case of roots is the formation of the growing points of lateral branches somewhat delayed and takes place from remains of the growing point which have retained the embryonic character. The main features of the formation of organs at the growing points have been dealt with in the section on Morphology. SYMMETRY and POLARITY have been considered on p. 74 ff.; these are often manifested even at the growing point. The contrast of base and apex which constitutes polarity is determined in the egg-cell in higher plants, and is as a rule maintained when once established. It must be pointed out here that all growing points do not arise from pre-existing similar ones. Development of the plant can proceed by restitution as well as by the normal organogeny.

By **Restitution** (55) is understood the new formation of organs which as a rule follows the mutilation of a plant, and can take place in situations where no active growth would have been manifested in an uninjured plant. The types of restitution may be distinguished as regeneration and reparation.

REPARATION is when the lost organ is again formed from the wounded surface. This kind of restitution, though not uncommon in lower plants such as Algae and Fungi, is of very restricted occurrence in the higher plants. Only tissues that are meristematic or embryonic, and by no means all of these, are capable of reparation. It is most frequently seen in the growing point of roots; when the tip is removed by a transverse cut, if this is not more than 0·5 mm. from the tip, it may be again formed. A longitudinally-split root-tip tends to completion by reparation, so that a root thus treated may obtain two growing points. True reparations do not occur at the growing points of shoots; they are rare in the case of leaf-primordia.

REGENERATION, on the other hand, is wide-spread among plants. In this case an organ which has been lost is replaced either by the

formation of a new one in the vicinity of the wound or the outgrowth of one which was in a rudimentary condition. Examples of this type of restitution are afforded by the Algae and Fungi, and especially by Bryophyta. These can only be mentioned here, and consideration will be limited to the Flowering Plants. The capacity to form roots is especially wide-spread. In Geraniums, Willows, and many other plants, roots can be induced to form at any point by cutting off the shoots. In other plants the roots develop at particular places such as the older nodes. After roots have developed, the stem gives rise to a complete plant either by the unfolding of axillary buds or by the development of new growing points of shoots. Separated leaves are often able to form roots, though the power of giving rise to a new shoot is rarely connected with this. Even separated roots, when they are able to give rise to shoots, may regenerate new plants. Regenerative buds may also arise on tendrils, flowers, and fruits. When in regeneration the production of shoots is not provided for by existing growing points, new ones may be developed. If the growing point of a seedling is destroyed a new growing point may be developed from the meristem above the youngest leaf-primordium. While the regeneration is here restricted to meristematic cells, in other cases older fully-grown cells may recommence to grow and divide and thus return to the meristematic condition. A special tissue, called CALLUS, is thus first formed at the wounded surface, and new shoots may form within this. In yet other cases fully-grown epidermal or parenchymatous cells may give rise to growing points directly, *i.e.* without the formation of callus. Fig. 257 shows the origin of a regenerative shoot from an epidermal cell of a leaf of *Begonia*.

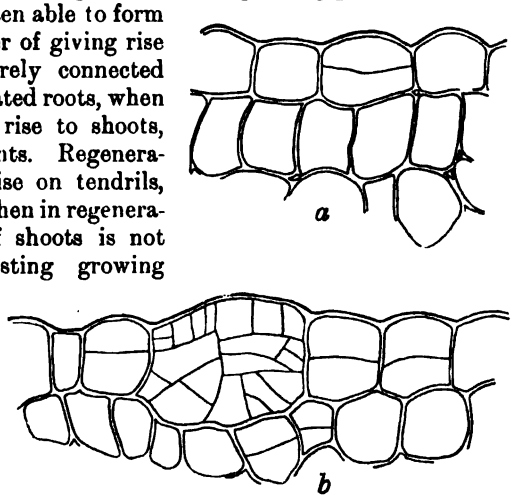


FIG. 257.—Transverse section of the leaf of *Begonia* showing the development of an adventitious shoot from an epidermal cell. *a*, The epidermal cell has divided once; *b*, a multicellular meristem has been produced. (× 200. After HANSEN.)

Tissues may also be regenerated from mature parenchymatous cells. Thus when the conducting tracts are interrupted new vessels may be formed from the parenchyma and re-establish the connection. The tissues which have been removed or interrupted are, however, not always formed anew; frequently substitutionary growth takes place. Thus, as a rule, an epidermis is replaced by cork, and it is exceptional for a true epidermis with stomata to be regenerated (58).

The new formation of epidermis, which occurs in the normal course of development in certain Araceae with perforations in their leaves, may be referred to here. In *Monstera deliciosa* particular limited regions of the laminae of quite young leaves die. Around these spots the mesophyll divides and forms from the outermost layer of cells a secondary epidermis, clothing the perforations and connecting with the primary epidermis of the upper and lower surface of the leaf. In the normal development of plants many processes which can be regarded as regenerative take place such as repeated cork-formation (p. 163).

In addition to the fact that regeneration occurs, the question as to where this takes place is of interest. The polarity which exists in the intact plant is frequently manifested in regeneration. Thus shoots tend to appear at the apical end and roots at the basal end of portions of stems, while the opposite distribution is found in roots. In more lowly-organised plants polarity is often apparent in the regenerative process, as when each of the single cells separated from a *Cladophora* forms a colourless rhizoid at the base and a green filament at the apical end.

This contrast of base and apex does not appear in regeneration from foliage leaves; this may be connected with the fact that the regenerating leaf is not included in the new formation. Frequently a new plant arises at the base of the leaf, which then dies off. Sometimes regeneration proceeds from the general surface of the leaf (*Torenia*), but frequently the place of regeneration can be determined by cutting the lamina, the new plants forming above the incisions (*Begonia*, Fig. 258).

The phenomena of regeneration have great importance in horticulture, since they allow of plants being rapidly multiplied without the aid of seeds. In artificial reproduction detached pieces of plants are made use of for the purpose of producing fresh complete plants. In many cases this is easily done, but in others it is more difficult or even impossible. The favourite and easiest method is by means of CUTTINGS, that is, the planting of cut branches in water, sand, or earth, in which they take root (*Oleander*, *Pelargonium*, *Tradescantia*, *Fuchsia*, *Willow*, etc.). Many plants may be propagated from even a single leaf or portion of a leaf, as, for instance, is usually the case with Begonias. In other cases the leaves, while still on the parent plant, have the power to produce adventitious buds, and in this way give rise to new plants. The Dandelion possesses the capability of developing from small portions of the root, and to this peculiarity is due the difficulty with which it is destroyed.

(b) Elongation.—The meristematic primordia require to enlarge and unfold before they can become functional, and this increase of size is effected in a peculiar and economical fashion. It results mainly from absorption of water from without. Organic material is of course required for the extension of surface of the cell walls, but there is no need of an increase in protoplasm during the enlargement. There is a great difference in this respect between the growth of a plant and a typical animal; nothing corresponding to this "phase of elongation" is met with in the latter.

The meristematic cells of the growing point contain considerable amounts of imbibed water in the wall and protoplasm. As absorption of water from without continues, a distinction becomes evident between the fully-saturated protoplasm and the vacuoles filled with a watery solution; this leads ultimately to the single large central vacuole or sap-cavity surrounded by the peripheral layer or sac of protoplasm (cf. p. 12, Fig. 3). It has been already seen (p. 225) that the vacuole is the seat of osmotic forces; the turgidity of the cell is essential to the growth in surface of the cell wall.

FIG. 258.—Leaf of *Begonia* used as a cutting and bearing regenerative shoots. (After STOPPEL.)

Cells in which the turgescence has been destroyed by plasmolysis (p. 226) exhibit no further growth, and it might be concluded from this that the mechanical distension of the wall assists or renders possible its growth. No clear correspondence between distension and growth can, however, be assumed to exist. Moreover, the pressure of turgescence cannot be replaced by mere mechanical stretching of the wall. The protoplasm plays the main part in the growth in surface of the cell wall, and in connection with this it can be understood how the walls of cells that are only slightly distended may grow rapidly.

Regarding the processes in the growth of cell wall which are termed apposition and intussusception, what is necessary has been stated on p. 35. In growth in surface due to plastic stretching without addition of material, followed by the addition of new layers to the wall, the stretching due to turgor appears as a natural preliminary to the growth. In the case of growth by intussusception the turgor pressure appears less necessary.

With the increased absorption of water following on the growth of the wall

the cell sap must become more dilute. This does not actually occur owing to the power of the growing cell to regulate the osmotic pressure of the cell sap. The pressure can be increased by the transformation of sugar into organic salts; thus, for example, by a change of glucose into oxalic acid the osmotic pressure can be trebled. On the other hand, the pressure can be lessened, *e.g.* by complete combustion of sugar in respiration.

Besides the expansion in the longitudinal direction, expansion in a transverse plane (growth in thickness) has to be considered. The diameter of the mature root or stem is often considerably greater than that immediately behind the growing point. As has been seen on p. 140, a distinction is drawn between primary and secondary growth in thickness. Only the primary growth in thickness is a phenomenon of the kind that is here being considered. In secondary growth new meristematic cells are formed from an intercalary meristem or cambium, and only later pass into a phase of expansion.

TISSUE TENSIONS.—The expansion of the cells in length and breadth does not always take place uniformly and simultaneously in the whole cross-section of an organ. It is usual to find that, in growing stems for instance, the pith strives to expand more strongly than the peripheral tissues. Since no breach of continuity between the two regions is possible, a state of tension (tissue tension) results. The pith expands the cortical tissues and these compress the pith; the actual length of the organ is the resultant of these antagonistic tendencies. If the tissues are artificially separated, each assumes its own specific length; the pith elongates and the cortex contracts and the tension disappears.

The tissue tensions which occur generally in growing organs may be demonstrated in this way. In a sunflower shoot the pith is separated for some distance from its connections to neighbouring tissues by means of a cork-borer. On withdrawing the cork-borer the cylinder of pith projects for some distance from the cut surface of the stem (Fig. 259, *1*). If a similar shoot is split longitudinally the two halves curve outwards owing to the elongation of the pith and the contraction of the epidermis. Even in the case of hollow shoots such as the stalk of the inflorescence of the Dandelion (*Taraxacum*) a tension exists between the outer and inner tissues which is expressed by curvatures when the stalk is split longitudinally (Fig. 259, *2a*). If the stalk after this treatment is placed in water the curvature increases considerably (Fig. 259, *2b*).

Tissue tensions also occur in leaves and roots. The tensions need not be in the longitudinal direction alone; there are also transverse tensions. Thus, for example, the rind of trees which increase in thickness by secondary growth is considerably stretched in the tangential direction. On being separated from the wood it therefore contracts.

The tissue tensions gradually arise at some distance from the growing point when the expansion of cells is commencing, and as a rule they again disappear in the fully-grown zone, though they persist in the case of some organs. They are of great importance for the rigidity of growing tissues; they increase the rigidity given by the

turgescence of the individual cells. The tissue tension presents a certain resemblance to the turgescence of the cell; this is most evident in the typical stem. Just as the cell sap distends the cell wall by its osmotic pressure, the expanding pith stretches the cortical tissues. Increased resistance to deformation and increased rigidity result from the stretching of the cortex, just as they do in the cell from the stretching of the wall.

The tissue tension ceases as all the cells attain the permanent mean length dictated by the size of the organ. Sometimes, however, certain cells after attaining their greatest length exhibit a considerable contraction associated with an alteration in shape. This occurs often in roots when the tissues of the cortex and of the central portion are thrown into folds by the contraction of the tissue that lies between them. The significance of this contraction of roots, which may lead to a shortening of the fully-grown structure by 10-70 per cent, is very great. Thus it is due to it that the leaves of many "rosette plants," in spite of the continued growth in length of the stem, remain always appressed to the soil. It determines and regulates the penetration of many tubers and bulbs to a definite depth in the soil. It increases the fixation of the plant in the soil, since greater stability results from tense than from slack roots.

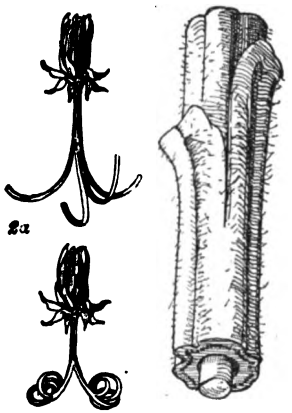


FIG. 259.—*1*, Shoot of *Helianthus annuus* with the leaves removed and the pith separated from the peripheral tissues by means of a cork-borer. *2*, Stalk of the inflorescence of *Taraxacum*, split longitudinally by two incisions at right angles to one another; *a*, just after splitting; *b*, after immersion in water.

(c) Internal Differentiation.—The cells of the typical growing point maintain their power of growth and division; they are termed meristematic cells. All organs composed of such cells have in principle the capacity for unlimited growth. Embryonic tissue is found not only at the growing points, but in the secondary meristems (p. 47).

A portion of the meristematic tissue, or the whole of it in the case of organs of limited growth, becomes transformed into the somatic cells of the permanent tissues; in these growth and cell division cease, and sooner or later death ensues (p. 309).

The internal development of an organ commences close behind the growing point and lasts for a longer or shorter time. While the full development of hairs is frequently very rapid, the definite form and structure of the internal tissues is often only completed after the phase of elongation is ended. When secondary growth in thickness takes place there is no termination to the internal development. The development

of the "permanent tissues" from the primary and secondary meristems has been described in the morphological section. Here it is only necessary to recall the fact that the following processes are concerned; in the first place the formation of cells by cell division which takes place in the embryonic tissues and at the commencement of elongation; following on this the separation of cells which gives rise to intercellular spaces; the independent growth of the individual cells; thickening and chemical changes of the cell walls; modifications (and eventually in some cases the complete disappearance) of the cell contents; and lastly fusions of cells (cf. p. 44).

In the arrangement of the tissues the same symmetry, which is apparent in the external form of the organs of the plant, is seen; the internal structure of the organs is thus radial, bilateral, or dorsiventral.

II. The Factors of Development

In attempting to determine the factors which influence development it is necessary to treat of examples which show in characteristic fashion the effect of particular factors. Completeness, either in the enumeration of the factors or as regards their influence, is out of the question. It is advisable to select the simplest influences when possible, since more complicated cases require further investigation. As in other cases the factors may be divided into the two groups of external and internal factors.

A. External Factors

All the forces and substances which have been seen to be physiologically effective in the metabolism, or which play a part in movements, are among the external factors of development.

Certain external factors were mentioned on p. 218 as general conditions of life; without these it is evident that no development would take place. These, and other factors which are not necessary, exert a profound influence on growth. Quantitative and even qualitative changes in the organs of plants may be educed by variation in the intensity, quality, or direction of such factors. These influences, in which the connection between cause and effect is always complicated and involves stimulation of the protoplasm, are termed formative.

1. **Temperature.**—As in the case of metabolism it is found that a certain temperature is a necessary formal condition of growth.

There is complete cessation of growth at a temperature less than 0° or higher than 40°-50°. Between the MINIMUM and MAXIMUM temperatures, at which growth ceases, there lies an OPTIMUM temperature at which the rate of growth is greatest. This optimum

temperature usually lies between 22° and 37° C. Plants inhabiting different climates exhibit considerable differences in regard to the cardinal points for temperature (cf. p. 219). That the different individuals of the same species may show great differences in the dependence of the phase of elongation on temperature is seen in the unequal development of the buds of the Horse-chestnut, etc., in spring. Even in the same individual the processes of growth in the different organs are variously influenced by the temperature.

In tropical plants the minimum temperature may be as high as + 10° C., while those of higher latitudes, where the first plants of spring often penetrate a covering of snow, as well as those of the higher Alps and polar regions, grow vigorously at a temperature but little above zero. Many of our spring plants show that the opening of their flowers can take place at a lower temperature than the unfolding of the foliage leaves.

2. Light.—The growth of a plant is rarely so strictly limited to a particular illumination as to a particular temperature. There are, however, some organs in which growth commences only after a certain intensity of light has been experienced; some seeds (p. 305) and all parts of plants which are normally exposed to light can only continue their development when this is present. Long-continued darkness produces an abnormal growth, in that the normal correlation between different organs is disturbed; the growth of certain organs is unduly favoured, and of others greatly retarded. In darkness the yellow pigment of the chloroplasts but not the chlorophyll is formed. The stems of Dicotyledons, in such cases, become unusually elongated, also soft and white in colour. The leaf-blades are small and of a bright yellow colour, and remain for a long time folded in the bud (Fig. 260 *E*). A plant grown under such conditions is spoken of as ETIOLATED.

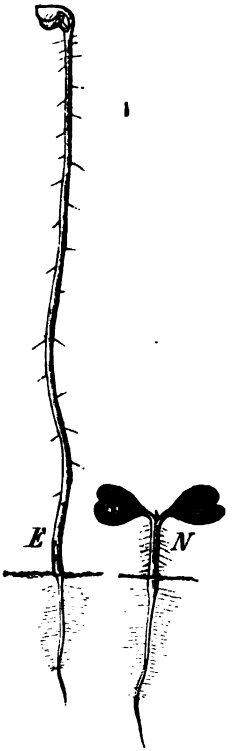


FIG. 260.—Two seedlings of *Sinapis alba* of equal age. *E*, Grown in the dark, etiolated; *N*, grown in ordinary daylight, normal. The roots bear root-hairs. (After NOLL.)

The elongation of certain organs and simultaneous reduction of others has an ecological significance in nature in the case of seedlings and rhizomes which are growing in the dark. The parts which are functional only in the light remain at first undeveloped, and the constructive material for them and especially for the chlorophyll is economised. The great elongation of the other organs which is mainly dependent on an accumulation of water brings the parts that need it as soon as possible into the light.

Comparison of an etiolated plant with one grown in the light shows that the influence of light is not the same on all organs; it may either increase or arrest the growth. While, however, the action of light in arresting the growth of the stem increases with the intensity, the increase of the growth of leaves due to the light has a limit; the leaf attains its maximal size in light of moderate intensity. It is a one-sided view of the growth in length of the stem, and the resulting height of the plant that is expressed by the statement, "the effect of illumination is to retard growth." In these organs, and in others that behave similarly, the effect of light is found to be much less simple. It appears rather, as is shown by the accurately-investigated case of the coleoptile of *Avena*, that light first accelerates and then retards growth, and that both influences increase with the intensity of the light. With every increase in the illumination there is first acceleration and then retardation of growth, while on darkening the plant there is retardation followed by acceleration ([57]).

The effect of the component rays of white light appears to be still less simple. When light is arresting the elongation of the stem it is the blue and violet rays of short wave-length that are effective, while the red rays behave in the same way as darkness. Other processes of growth, however, are influenced differently. The germination of the spores of certain ferns is accelerated by red light, while blue light hinders it even more than darkness. Spores germinated in red light produce greatly elongated cells which only become divided by cell walls in blue light ([57a]). The complicated nature of the phenomena is in part explained by light acting both as a stimulus to growth and as a source of energy. Ultra-violet light injures the plant; radium- and Röntgen-rays retard, but, like poisons (p. 29 4), may when in small quantity promote growth ([58]).

In addition to the intensity and the quality of the light, its direction greatly influences the form of the plant body. The curvatures due to one-sided illumination (phototropism) will be dealt with later in connection with the phenomena of movement. The illumination may also influence the polarity and symmetry of the plant. Thus in some simply-organised plants the more strongly illuminated side of the cell from which development starts becomes the apex and the other side the base. In other cases an originally radial growing point becomes bilateral or dorsiventral under one-sided illumination. Lastly, an organ which has passed the embryonic stage may become dorsiventral, as in cases where roots form on the shaded side only. When it is possible to experimentally transform the external symmetry the internal structure is also as a rule altered, the connection between the two being very close.

In the germination of the spores of *Equisetum*, the first division wall, and with this the distinction of apex and base, is determined by the direction of the light.

A similar influence of light on the polarity is shown by the egg-cells of *Fucus* and *Dictyota*.

Antithamnion crucialum, one of the Florideae, forms decussately-arranged branches when in diffused light; on one-sided illumination the branches all stand in one plane at right angles to the direction of the rays. Further examples of dorsiventrality induced by one-sided illumination are afforded by the branches of many Mosses, the thalli of most Liverworts, and the prothalli of Ferns; these structures in the absence of such illumination are sometimes radial and in other cases bilaterally symmetrical. In fern prothalli and the thallus of *Marchantia* the dorsal side is determined by the stronger illumination. In the case of the prothalli, when the lower side is illuminated, the new growth is adapted to the altered direction of the light and the former upper side becomes the lower; in the Marchantiaceous thallus, on the other hand, the dorsiventrality once induced cannot be changed. The shoots of Ivy and other root-climbers in which the climbing roots are produced on the shaded side may be cited as an example of dorsiventrality induced by light in the higher plants.

Comparison of an etiolated and a normal plant shows that influence of the intensity of the light under which the plant has grown extends to the internal structure. The tissues of the etiolated plant are less differentiated and thickened cells are wanting. A less complete contrast than between light and darkness may be effective. Shade-leaves (b9) have a very different structure from the leaves of the same species developed in full sunlight. They are thinner, their palisade cells narrow below, leaving wide intercellular spaces between them, and form only a single layer; in sun-leaves the palisade cells are longer and form several layers.

Alpine plants, the illumination of which differs in duration, intensity, and composition from that in the plains, differ in their whole habit from lowland plants. Their vegetative organs are contracted, while the flowers are large and brightly coloured. Other factors than light are concerned in this change.

3. Gravity.—A plant can readily be removed from the light but gravity is always acting upon it. It is only possible to change the direction of its action. When the direction of the action of gravity coincides with that of the main shoot and root of the plant no effect is perceptible; when it forms an angle with the line of these organs curvatures are produced (see Geotropism), as in the case of illumination from one side. Apart from these curvatures an action of gravity on the polarity of the plant is established; this does not amount, however, to inversion or to the transformation of the shoot into a root. There is no case of the polarity of the undifferentiated egg-cell being altered by gravity; this is always determined by internal causes, though gravity may have a modifying influence.

If twigs of Willow are cut and suspended in a moist chamber roots form near to the lower end, while only the buds situated near the other end expand into shoots (Fig. 261, 1). If the twig is hung in the inverted position it is the corresponding buds at the end which is now lowest which still give rise to shoots, while the strongest roots are produced near to the lower end which is now uppermost (Fig. 261, 2). This experiment shows that internal causes mainly determine the contrast of the two poles. Since, however, in the inverted position there is a displacement downwards of root-formation and upwards of the unfolding of the

buds gravity must also play a part. It has, however, in no case proved possible to effect a complete and lasting inversion of the polarity of a plant in this way; while such inverted plants may live for a considerable time, they exhibit serious disturbances in their anatomical construction ([59a]).

An effect of gravity on the internal disposition is also seen in the case of obliquely or horizontally placed branches. The tendency of the internal disposition is to cause the uppermost buds to develop and give rise to long shoots. On branches displaced from the vertical the basal buds are favoured and the more apical buds arrested. When the branch is curved the strongest branches arise at the highest point of the curve. In the cultivation of vines and fruit trees this peculiarity is utilised to produce shorter and weaker shoots (short shoots), which experience has shown are those that bear the flowers.

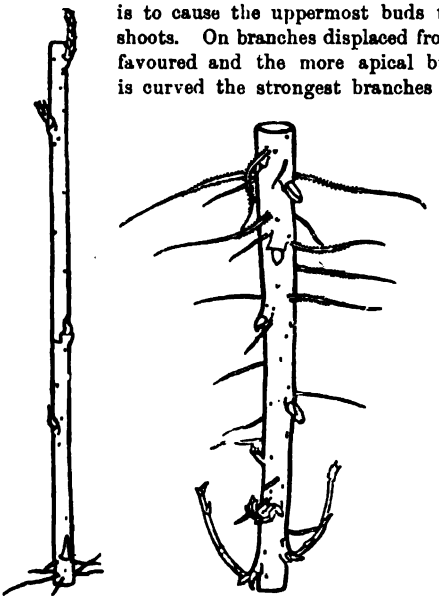


FIG. 261.—Twigs of Willow: 1, in the normal position; 2, in the inverted position growing in a moist chamber. (After VOCHTING.)

4. Mechanical Influences. — Pressure and traction exert a purely mechanical influence upon growth, and also act as stimuli upon it. External pressure at first retards growth; it then, however, stimulates the protoplasm and occasions the distension of the elastic cell walls, and frequently also an increase of turgor. As a consequence of this increased turgor, the counter-resistance to the external pressure is intensified. If the resistance of the body exerting the pressure cannot be overcome, the plasticity of the cell walls renders possible a most intimate contact with it; thus, for instance, roots and root-hairs which penetrate a narrow cavity fill it so completely that they seem to have been poured into it in a fluid state. It would be natural to suppose that the effect of such a tractive force as a pull would accelerate growth in length by aiding and maintaining turgor expansion. But the regulative control exercised by the protoplasm over the processes of growth is such that mechanical strain first acts upon growth to retard it, but then causes an acceleration of even 20 per cent.

Other actions of mechanical influences as stimuli may be mentioned. Lateral roots arise only from the convex sides of curved roots (Fig. 262), the cause lying probably in the DIFFERENCES OF TENSION between the two sides. The primordia of the haustoria of *Cuscuta* and the adhesive discs on the tendrils of some species of *Parthenocissus* are caused to develop by the STIMULUS OF CONTACT.

If mechanical effects lead to wounding the result may be the phenomena of healing (p. 164) or restitution (p. 282).

5. Chemical Influences.—The presence of the necessary nutrient substances in sufficient quantity and the absence of poisonous substances are formal conditions for growth. While it is known that particular, essential, nutrient materials are not replaceable by an excess of others, some substances may be of special importance in particular processes. Since elongation is essentially due to the introduction of water, the significance of the water supply to a growing plant is obvious. Growth often ceases when there is not sufficient water in the soil. Even a diminution in the humidity of the air may arrest growth by increasing transpiration. Some plants, however, can store water, and are therefore more independent of its direct absorption. They grow at the expense of the stored water, and can often withdraw the water from older portions so that these wither while growth goes on at the apex, as is shown by potatoes sprouting in a dark cellar. Plants in damp situations are usually larger than those grown in dry places, and in fact may differ from them in their whole habit and mode of growth. A local excess of water in the plant, such as may be brought about by arresting transpiration by a coating of paraffin oil, may lead to various departures from the normal structure ([59b]).

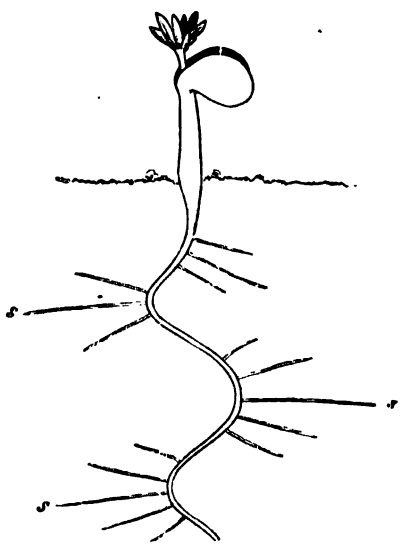


FIG. 262.—Young plant of Lupine, the main root of which has become curved. The lateral roots have arisen on the convex faces of the curves. (After NOLL.)

A striking stimulus-effect results from permanent contact with liquid water in such plants as can endure this. This is doubtless the result of the combined effect of a number of factors and not simply to the material effect of the water. Thus both the arrest of transpiration and the change in the illumination are of importance.

Amphibious plants, that is such as are capable of living both upon land and in water, often assume in water an entirely different form from that which they possess in air. This variation of form is particularly manifested in the leaves, which, so long as they grow in water, are frequently linear and sessile or finely dissected, while in the air their leaf-blades are much broader and provided with petioles (cf. Fig. 128). The leaf-stalks and internodes also often exhibit a very

different form in air and water, and undergo the same abnormal elongation as in darkness. This is especially noticeable in submerged water plants, whose organs must be brought to the surface of the water (stem of *Hippuris*, leaf-stalk of *Nymphaea*). Such plants are enabled by this power of elongating their stems or leaf-stalks to adapt themselves to the depth of the water, remaining short in shallow water and becoming very long in deep water.

The water-forms also differ from the land-forms in their internal structure. Thickened cell walls are frequently absent from the stem, and the vascular bundles are reduced; the leaves resemble shade-leaves. The most marked contrast to water plants is presented by such land plants as are exposed to insufficient water supply or too active transpiration. In these the vascular bundles are strongly developed, while the epidermis has the arrangements which have been considered under the means of protection against excessive transpiration.

In addition to the true nutrient materials which are employed in the construction of the substance of the plant, oxygen requires to be mentioned. Although its entry into the plant is connected with a loss of organic substance, it is quite indispensable for growth on account of the need of respiration. In aerobic plants at least, growth ceases completely on the withdrawal of oxygen; a diminution or increase of the proportion of oxygen in the air also influences growth.

Stimuli of the most various kinds proceed from substances acting on the plant.

Poisons must first be mentioned; these are substances which in very dilute solutions arrest growth and ultimately life. Thus even in a dilution of 1 in 25,000,000 copper sulphate kills such Algae as *Spirogyra* and also peas in water cultures. It is a striking fact that many poisons when in extreme dilution have a stimulating effect on growth. Chemical stimuli due to other substances play a large part in the germination of many seeds, spores, and pollen grains, and in the development of fruits. Some pollen grains only germinate when they obtain traces of substances which are present on the stigma. Many parasitic fungi and also parasitic Phanerogams (*Orobanche*, *Lathrea*) are stimulated to develop by unknown substances proceeding from their hosts. In Algae and Fungi high concentration of some food materials may give rise to striking changes in form.

6. Influence of Foreign Organisms.—Fungi and Bacteria living parasitically in flowering plants often cause profound deformations that are known as GALLS (60). In the simplest cases there is merely a hypertrophy of cells, while in more complex ones there are qualitative changes in the organ. Still more striking gall-formations are caused by animals, especially insects. Outgrowths form, which serve the parasites for protection and food. The structure of the gall appears purposive when considered from the side of the parasite, the protective layers and nutritive layers of the gall being without significance for the plant.

Euphorbia Cyparissias, when attacked by a rust fungus (*Aecidium Euphorbiae*), becomes sterile, remains unbranched, has shorter and broader leaves, and in its whole appearance is so changed as scarcely to be recognisable. Plant lice sometimes cause a flower to turn green, so that instead of floral leaves green foliage-like

leaves appear. Another peculiar example of abnormal growths is afforded by the GALLS or CECIDIA produced on plants by Fungi, or more frequently by insects, worms, and arthropods. The effect of these formations on the normal development of the tissues of a plant is more or less disturbing, according to their position, whether it be in the embryonic substance of the growing point, in the tissues still in course of differentiation, or finally in those already developed. Galls which are products of abnormal tissue formation are termed HISTOID, while ORGANOID galls depend on the transformation or new formation of members of the plant body. The latter are especially instructive. The larvae of *Cecidomyia rosaria* live in the growing points of Willow stems, and occasion a malformation of the whole shoot by the production of galls, known as "willow-roses," which are composed of modified leaves and axes. Flies (Diptera) often deposit their eggs in the tissues of partially-developed leaves, in consequence of which the leaves become, according to their age when attacked, more or less swollen and twisted. After the leaves of the oak have attained their full growth they are often stung by a gall-wasp of the genus Cynips. The poison introduced by the sting, and also by the larvae hatched from the eggs deposited at the same time, occasions at first only a local swelling of the leaf tissue, which finally, however, results in the formation of yellow or red spherical galls on the lateral ribs on the under side of the leaf.

Symbionts, *i.e.* associated, mutually-beneficial organisms, neither of which can be regarded as the host, may influence one another formatively. This is seen, for example, in Lichens.

It is probable that chemical substances play an important part in the influences exerted by one organism on another. It is true that only in rare cases have deformations resembling galls been brought about by the action of dead substances extracted from the normal inhabitant of the gall. Parasites which do not give rise to galls probably act on the host plant by poisonous substances. On the other hand, the host plant by forming anti-bodies may injure the parasite or prevent its entrance. Thus HEINRICHER has shown that some kinds of pear-tree are readily infected by the mistletoe and others only with difficulty; he has also shown that probably one infection by the parasite renders the host more resistant to artificial infections. There are thus PHENOMENA OF IMMUNITY in the vegetable kingdom, though they have not been nearly so thoroughly investigated as in the case of animals ([60a]).

7. Purposiveness of the Reactions to External Factors.—It has been seen that the form and structure of the plant is influenced in a regular fashion by many external factors. While some of the resulting changes are without importance to the plant or, as in the case of galls, are only of use to the organism causing the change, the majority of reactions to external stimuli are remarkably purposive, *i.e.* they are of use to the plant. Examples are afforded by the elongation in etiolation, the characteristic development of amphibious plants in water and on land, the increase of protections against transpiration with the greater dryness of the atmosphere, etc.; these purposive reactions are termed ADAPTATIONS. How it comes about that the

plant frequently reacts in a purposive fashion will not be considered here (cf. p. 212).

B. Internal Factors

When a change occurs in an organism while all the external factors remain constant it must be referred to internal factors. The latter cannot be so readily analysed as the external factors, so that the reference of many phenomena to internal factors is frequently little more than a statement of our ignorance.

1. Determinants.—The determinants which a plant has derived from its parents are the first internal causes to be mentioned; it is these that lead to the regular origin of a fungus from a fungal spore or of a bean-plant from a bean-seed. In particular they determine the agreement of all the individuals of any species, when under the same external conditions, in such characters as the colour of the flower, form of the leaf, size, etc. It is not as a rule possible to experimentally alter the determinants possessed by a species, and they cannot be ascertained by direct observation On this account further consideration of them may be deferred until heredity is treated later.

2. The Phenomena of Correlation ([61]).—While external factors have a profound influence on the internal structure of plants the differentiation of tissues proceeds under quite constant external conditions; it is thus determined by internal causes. We do not know what is the nature of the particular causes that force a meristematic cell into a definite course of development. Only one thing is certain; from every cell of the growing point everything might arise, all the cells agreeing in their determinants. It is the mutual connections or correlations between the cells that lead to the lines of development followed by this and that cell. When these connections are removed it has been seen in the phenomena of reparation (p. 282) how cells exhibit quite other capacities than those they had previously shown when in connection with one another. This applies to mature as well as meristematic cells when their connection with neighbouring cells is interfered with. Thus in the process of regeneration (p. 282) it has been seen how fully-grown cells that would soon have perished again become young, and how, for example, from a single epidermal cell all the various cells characteristic of the particular plant can be derived. It is clear that an organism in which such mutual action of the cells was lacking could not exhibit the division of labour that is customary in the higher plants. In other words, correlations must be reckoned among the "regulations" without which the organism is inconceivable.

Such correlations exist between the externally visible organs of a plant as well as between its cells. This, if not as a rule evident, becomes apparent when an organ is removed and the reactions of the isolated organ and of the plant from which it was taken are studied,

or when an organ is experimentally brought into a position it did not previously occupy.

The first result of the removal of an organ may be the appearance of so-called COMPENSATIONS; other remaining organs become larger. The leaves which arise at the growing point prevent older leaves attaining their maximal size, and if the growing point is removed the size of the leaf may be increased (*e.g.* in the tobacco plant). The active development of some of the axillary buds hinders that of many others; if the dominant shoot is removed the resting buds commence to grow. The conclusion may be drawn that even in normal development the size of the organs is determined by correlative influences from neighbouring organs. In other cases a QUALITATIVE effect follows the removal of an organ. If the tip of a Pine is removed, its place is taken by one of the adjacent lateral branches, which assumes the erect position and shows the same leaf arrangement as the original main shoot. It appears that the usual oblique position and dorsiventral arrangement of the foliage on the lateral branches comes about under the influence of the main shoot. In this and many other cases of correlative influence it is not necessary that the organ should be removed; as a rule it is sufficient to interfere with its normal action, as for example by embedding it in plaster of Paris.

It has been shown in treating of restitution (p. 282) that new roots or shoots may be produced on isolated organs. Thus the members of the plant, like every cell, are originally capable of further development in a number of directions. It is their mutual influence that serves to control this.

The effect of correlation is also shown when an organ is transplanted to a new position. By methods of transplantation, which have been derived from horticultural practice, it is easy in the case of many plants to make a separated part grow in relation to a wounded surface. The separated part is termed a graft, while the plant upon which it is inserted is called the stock. The graft may be of the same species as the stock, or from a related kind of plant. One correlative influence which is apparent is the suppression of regeneration on the part both of the stock and the graft. The latter adopts the root-system of the stock, while the stock in turn adopts the shoot-system of the graft; there is no necessity for the formation of new organs.

Artificial GRAFTING, like artificial propagation, plays an important part in horticulture. Separated shoots bearing buds serve as the grafts or scions, and are caused to unite with a rooted plant as the stock. In this way it is possible to obtain examples of considerable size of a race or species more rapidly than by seeds or by artificial propagation. In practice several different methods of inserting grafts are in use, but only the more important can be mentioned here. GRAFTING is the union of a shoot with a young and approximately equally-developed wild stock. Both are cut obliquely with a clean surface, placed together, and the junction protected from the entrance of water and fungi by means of grafting wax (Fig. 263 *II*). Cleft or tongue grafting is the insertion of

weaker shoots in a stronger stock. Several shoots are usually placed in the cut stem of the stock, care being taken that the cambial region of the different portions are in contact, and that the cortex of the shoots is in contact with that of the stock. In other methods of grafting, the cut end of the shoot is split longitudinally and the cut shoot is inserted in the periphery, or a graft may be inserted in the cortex or in the side of the stock. In grafting in the cortex the flatly-cut shoot is inserted in the space cut between the bark and the splint wood (Fig. 263 *I*). In lateral grafting, the shoot, after being cut down, is wedged into a lateral incision in the stock.

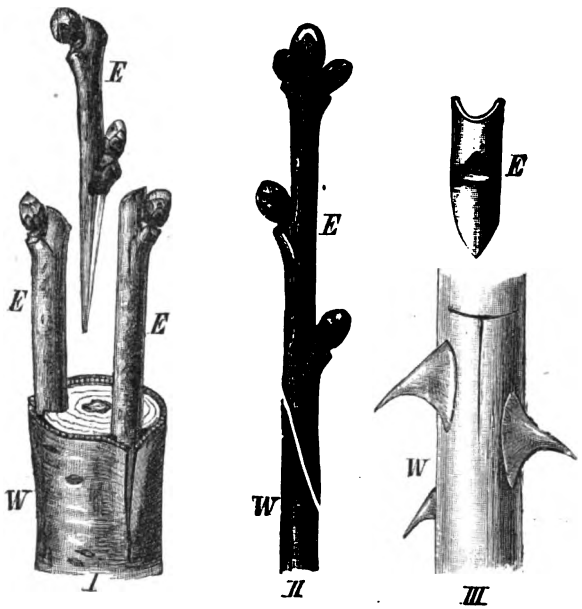


FIG. 263.—Different modes of grafting. *I*, Crown grafting; *II*, splice grafting; *III*, bud grafting. *W*, Stock; *E*, scion. (After NOLL.)

A special kind of grafting is known as BUDDING (Fig. 263 *III*). In this process a bud ("eye") and not a twig is inserted under the bark of the stock. The "eye" is left attached to a shield-shaped piece of bark, which is easily separated from the wood when the plants contain sap. The bark of the stock is opened by a T-shaped cut, the "eye" inserted, and the whole tightly covered. Occasionally some of the wood may be detached with the shield-shaped piece of bark (budding with a woody shield). In the case of sprouting buds, the budding is made in spring; in dormant buds, which will sprout next year, in summer.

The union is accomplished by means of a callus (p. 164), formed by both the scion and the stock. Vessels and sieve-tubes afterwards develop in the callus, and so join together the similar elements of the two parts. Such an organic union is only possible between very nearly related plants: thus, for example, of the Amygdalaceae, the Plum, Peach, Almond, and Apricot may readily be grafted one upon the other; or of the Pomaceae, the Apple with the Quince; but not the Apple with the Plum, nor (as has been asserted) with the Oak.

The polarity which is noticeable in phenomena of regeneration also influences the practice of grafting. Unlike poles of a plant may readily be induced to grow together, while like poles may only be brought to do so with difficulty, and then do not develop vigorously.

The stock and graft influence one another in a variety of ways. For example, portions of annual plants grafted on perennials attain an extended period of life; the opposite effect, a shortening of the life of the graft, may also result from grafting. Qualitative changes may also be brought about and may go so far as to lead to a vegetative bud of the graft becoming transformed into a flowering shoot. The specific properties of the two components are, however, maintained in cases of transplantation. Certain cases known as chimaeras appear at first sight to constitute an exception to this statement; fuller investigation, however, shows that while externally they appear intermediate formations between the symbionts in the graft, no mingling of the specific characters has taken place.

Chimaeras ([61a]).—Some plants grown in Botanic Gardens under the names *Laburnum Adami* and *Crataegomespilus* suggest in a number of ways comparison with hybrids (p. 317), but have undoubtedly not arisen by sexual reproduction. *Laburnum Adami* (Fig. 264) is intermediate between *Laburnum vulgare* and *Cytisus purpureus*; it frequently develops branches which can only be regarded as "reversions" to *Laburnum vulgare*, and less commonly others that completely resemble *Cytisus purpureus*. Certain intermediate forms between *Crataegus monogyna* and *Mespilus germanica* are known as *Crataegomespilus* or Bronveaux hybrids. The origin of these is known. The intermediate forms, of which several are known differing from one another, arose in the region of a graft of *Mespilus* on *Crataegus* in a garden at Bronveaux near Metz. It can be regarded as certain that the origin of *Laburnum Adami* was similar. Both plants have therefore been regarded as graft hybrids, *i.e.* as hybrids not resulting from the union of sexual cells, but by some influence of vegetative cells on one another.

More recently HANS WINKLER has produced such "graft hybrids" experimentally. He grafted *Solanum nigrum*, the Woody Nightshade, on *Solanum Lycopersicum*, the Tomato, and after union had taken place cut the stem of the stock transversely at the level of the graft. Among the adventitious shoots which developed from the region of junction of the two components there occurred well-marked intermediate forms. In the first instance there were forms which were composed of longitudinally-united halves with the characters of the grafted plants; these were termed chimaeras by WINKLER. Later there were obtained other intermediate forms, externally uniform (Fig. 265), which appeared to be the desired graft hybrids. Closer investigation showed, however, that these also were to be regarded as chimaeras, since they consisted of parts of the Tomato and the Nightshade intimately united in growth but otherwise unchanged.

FIG. 264.—*Laburnum Adami*, Poit (*Cytisus Adami*, Hort), with atavistic branches showing the characters of the two parental forms, *Laburnum vulgare* to the left and *Cytisus purpureus* to the right. (After NOLL.)

They were not longitudinally-united halves, however, but inner and outer layers of the growing point were formed of tissues of the two different species (cf. pp. 307 and 86). These have therefore been termed periclinal chimaeras in contradistinction to the sectorial chimaeras in which longitudinal segments are evident.

Cytisus Adami and the *Crataegomespili* are also periclinal chimaeras. True graft hybrids in which a mingling of the specific characters in a single cell has resulted from grafting are as yet unknown.

Solanum tubingese has the dermatogen of the Tomato, while the internal tissues are those of the Nightshade. The converse is the case for *Solanum Kölreuterianum*. In *S. proteus* the two outer layers are from the Tomato and the remainder from the Nightshade, while *S. Gaertnerianum* affords the converse condition (Fig. 265). In a corresponding fashion the dermatogen in *Cytisus Adami* is derived from *Cytisus purpureus* and the internal tissues from *Laburnum vulgare*. In one of the Bronveaux hybrids (the form *Asnieresii*) a core of *Crataegus* is covered by the epidermis of *Mespilus*; the other form (*Dardari*) has two or more enveloping layers from *Mespilus*. When adventitious shoots are developed from a single layer, these have the pure specific characters proper to the layer without any trace of admixture with the other symbiont.

Nothing is known with certainty of the mode of origin of periclinal chimaeras, but it can hardly be doubted that the growing points of these adventitious shoots are composed of cells derived from the two components, the one forming the core and the other the surface layers. WINKLER'S contention that there were also true graft hybrids is doubtful, and this author's own investigations show that the change in chromosome number in these plants is susceptible of another explanation. Further, the association of specifically different nuclei in the one cell, so long as they do not fuse, does not constitute a true hybrid but only a chimaera. Such a mixo-chimaera, which can again separate into its components vegetatively, has been experimentally produced in *Phycomyces nitens* by BURGEFF ([615]).

III. The Course of Development and its Dependence on External and Internal Factors

The course of development consists of a succession of processes which tend to be repeated in the same order in any particular kind of plant. Observations in nature suffice to show that this succession must be capable of modification. Deviations from typical form which are spoken of as monstrosities are not uncommonly met with. It is one of the objects of developmental physiology to ascertain the causes of such monstrosities, to produce them experimentally, and thus to arrive at some insight into the causes of normal development.

Although there are at present few of the phenomena of development which can be controlled experimentally, the results obtained force the conclusion upon us that THE TYPICAL COURSE OF DEVELOPMENT IS ONLY ONE AMONG A NUMBER OF POSSIBILITIES, THE OCCURRENCE OF WHICH IS DETERMINED BY A PARTICULAR COMPLEX OF CAUSES.

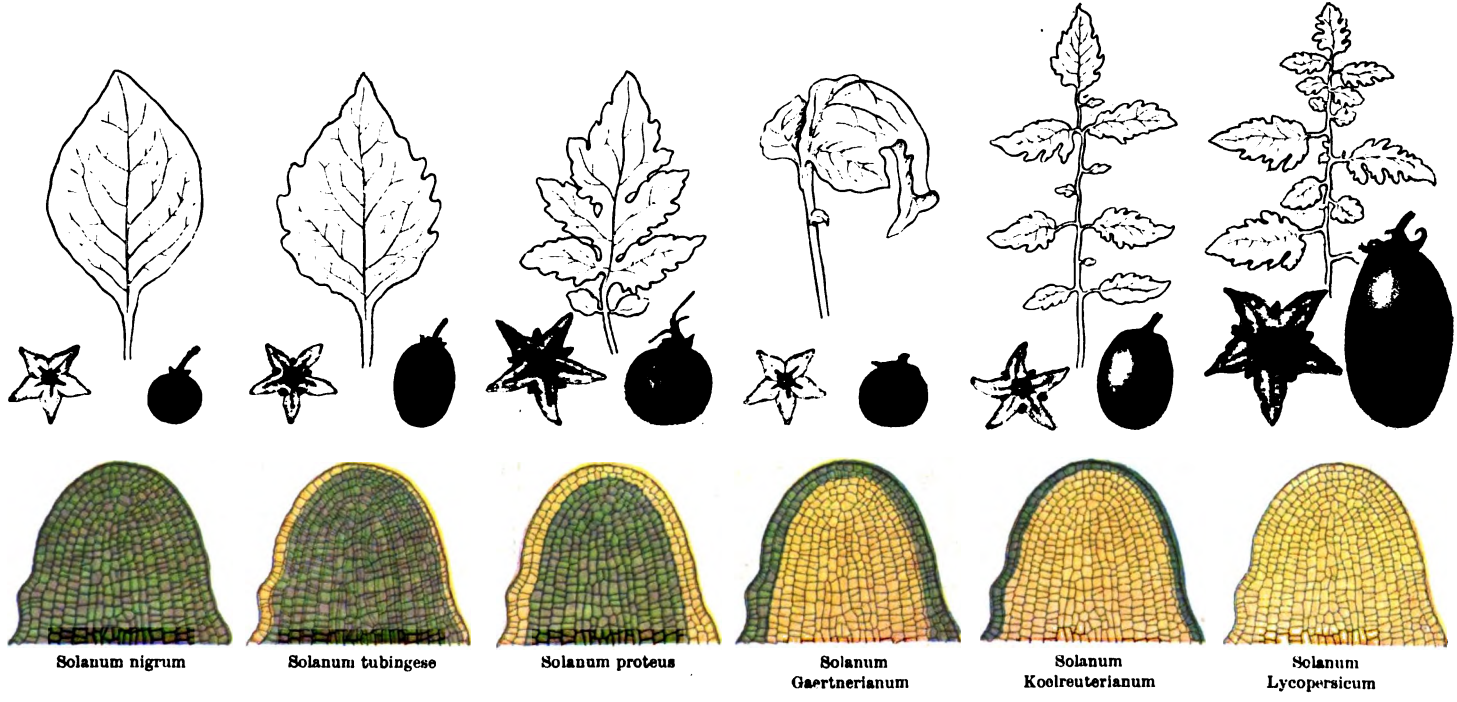


FIG. 265.—Graft chimaeras between *Solanum nigrum* and *Solanum Lycopersicum* together with the parent forms. In each case a leaf, a flower, a fruit, and a diagram of the growing point is represented. In the latter the layers derived from *S. nigrum* are coloured green, and those from the Tomato yellow. (Original by H. WINKLER.)

Every departure from this complex of causes will also find its expression in the form of the plant.

Alterations of the normal form tend to be more extreme the younger the cells are which are influenced. When the embryonic substance of a growing point is diverted from its normal course of development, a quite different structure may replace the one which was anticipated; in other cases intermediate forms of more or less monstrous appearance are developed. The embryonic substance of a growing point is still capable of giving rise to all the primordia which are included in the range of form of the species, and thus a vegetative shoot may arise in place of a leaf; in exceptional cases even the growing point of a root may continue its development as a shoot. On the other hand, the alteration of leaves that have commenced to develop is mainly restricted within the limits of the metamorphosis of the leaf; thus, for example, petals may be formed in place of stamens or carpels. The later the transforming influence takes effect on the primordium, the more incomplete will be its transformation.

All anomalous formations and functions of plants constitute the province of PHYTOPATHOLOGY (62); pathological morphology is concerned with the former. Monstrosities of external form are treated of under VEGETABLE TERATOLOGY (63) and the pathological alterations of the shape and contents of cells and tissues in the pathological anatomy of plants (64).

The development of an organism does not proceed always with the same activity or in continuous uniform growth. Usually periodic alterations are evident, resting periods alternating with others of active growth. During the latter, cell divisions periodically take place, various forms of leaves and shoots arise, and reproductive organs are developed; periodically also larger and smaller parts of the organism die off.

A. Resting Condition and the Commencement of Growth (65)

Attention has already been directed to the fact that three distinct states may be recognised in the plant: active life, latent life, and death. It was further pointed out that all the manifestations of life are at a standstill in the condition of latent life; the activities of metabolism, even respiration, are suspended, and there are no indications of growth and movement. The capacity of development still remains, however, and this distinguishes latent life from death.

Resting Condition.—The condition of latent life is met with in seeds, in the spores of some lower plants, and in many fully-grown parts and buds of plants during unfavourable periods of the year (cold periods, dry periods). It cannot be endured indefinitely by plants; even seeds and spores in which it is most complete lose sooner or later the capacity of development and die. In other cases, as in the

unfertilised egg-cell, growth is suspended, but all vital activities are not suppressed.

At first sight it appears as if the resting condition during an unfavourable season was caused thus. As a matter of fact, however, periodic cessations of growth are found in many tropical trees; while temperature and water-supply continue favourable, the leaf formation does not proceed continuously, but is interrupted by resting periods, so that there are several periods of active growth in the course of the year. In our native plants also the entry upon a resting period is in no way determined by the low temperature. The unfolding of the leaves of many trees ceases completely in May or June. Further, our trees, when transferred to a tropical climate, frequently exhibit a periodicity similar to the native plants of the new locality. These phenomena are not interpreted in the same way by all investigators. On the one hand it is assumed that every periodicity in the growth of a plant is determined by a periodicity in the environment which need not be in the supply of moisture and warmth, but may concern, for example, the absorption of nutrient salts. On the other hand it may be assumed that plants possess a periodicity depending on internal causes, and that they become adapted to the seasonal changes in countries where such occur; with us the resting period is the winter, while in other countries it occurs in the dry period. This does not hold for all plants, however. In our climate there are some herbs, such as *Senecio vulgaris*, which continue to grow throughout the whole year if the external conditions permit, and in the tropics plants which grow continuously also occur.

The Oak, Beech, Apple, and Pear retain their resting period in the sub-tropical climate of Madeira, while under uniformly favourable conditions in the mountain regions of Java the periodicity may be disturbed in particular individuals. This even occurs in the several branches of the same tree, which may then bear leafy and leafless boughs at the same time (Oaks, Magnolias, Fruit, and Almond trees, together with some endemic species). Other trees gradually accustom themselves to the new conditions, as the Peach, for instance, which in Réunion has become nearly evergreen in the first generation and completely so in the second. It does not appear to be known how the periodicity of the unfolding of its buds has been affected.

Commencement of Development.—The termination of the resting condition and the resumption of growth often depends only on the establishment of general conditions for growth. In other cases the resting condition is more fixed but may be sometimes shortened by particular stimuli.

The germination of seeds takes place as a rule when the general conditions for growth are present, especially the necessary temperature, supply of oxygen, and water; but examples are not wanting in which special stimuli are requisite. Such special stimuli, usually provided

in the process of fertilisation, are also concerned in removing the inhibitions on the growth of egg-cells.

Some seeds pass through a prolonged resting period before they commence to germinate. They may lie for years in the soil, while others of the same age have germinated long before; this in part depends on the hardness of the seed-coat and the consequent difficulty of swelling. This also appears to be the main reason why the seeds of many aquatic plants (66) will not germinate in pure water, but do so on the addition of acids or alkalies. In some cases fully swollen seeds are unable to germinate except in the LIGHT (67). The red and yellow rays are usually more effective than more highly refractive rays, and a surprisingly short exposure to illumination may suffice (*Lythrum salicaria*, $\frac{1}{10}$ second, at Hefner-Kerze intensity of illumination 730). Not uncommonly the illumination may be replaced by a particular high temperature or by chemical stimuli. The latter play the chief part in the case of certain parasites which only germinate in the vicinity of their host plants (*Orobanche*, *Tozzia*). In other cases (*e.g. Amarantus*) light hinders or delays germination, and darkness is an advantage.

In the case of spores also germination may begin on the establishment of the formal conditions of growth or may require special stimuli.

A striking and fixed resting condition is seen in deciduous trees. At a certain season of the year, in the autumn or earlier, their buds can in no way be induced to expand. Later, however, a considerable shortening of their resting period may be caused not only by a higher temperature but by a number of stimuli such as frost, heat, dryness, darkness, illumination, ether vapour, acetylene, tobacco smoke, wounding, injection of water, etc.

The awakening from the resting state (68) is most readily effected shortly before the normal resumption of activity, but almost as readily at an early period shortly after the period of rest has begun. In the intervening period of complete rest, attempts at removing the inhibition on growth are usually without effect. These relations have to be taken into consideration in the forcing of plants in horticultural practice.

The Stimulus of Restitution (69).—The causes of the commencement of growth in the case of restitutions have also to be considered. The answer appears simple, since the phenomena as a rule follow on wounding. The fact, however, that processes that resemble restitutions are met with in the course of normal development shows that circumspection is required. Thus, for example, young plants are developed in the indentations of the leaves of *Bryophyllum*, and in the case of certain Begonias shoots are developed from the intact as well as from the incised leaf-blade. It has been shown experimentally that for many true restitutions it is not the removal of an organ but the interruption of its functions that is required to start the new growth (p. 297).

Polarity.—The fertilised ovum of the flowering plant, when the inhibition on its growth is removed, forms two distinct growing points for the shoot and root respectively. A corresponding polar

differentiation with the distinction of apex and base is met with also in more simply-constructed plants. While cases have been already referred to in which this distinction is determined by an external factor, in all higher plants the polarity is specific and depends on internal causes. We can neither cause growth with polarity in a spherical apolar Alga, nor induce a higher plant that possesses polarity to become apolar.

The polarity once it has been defined in the egg-cell is on the whole maintained throughout growth. In some plants, however, it can be seen to be altered from internal causes.

Thus in species of *Platycerium* and *Adiantum* among the Ferns and in *Neottia nidus avis* among the Orchids, shoots are formed directly from the growing points of roots. In the Adder's-tongue Fern (*Ophioglossum*) the vegetative reproduction depends entirely on the formation of buds close to the growing points of the roots. The apex of some fern leaves also (*e.g. Adiantum Edgeworthii*) may grow directly into a shoot.

Symmetry.—Every growing point effects in a characteristic fashion the further construction of the organ to which it belongs, and also provides the primordia of lateral organs, the distribution of which as they appear is definitely determined, and may be radial, bilateral, or dorsiventral. Thus a certain symmetry already exists in the growing point, and, at least in many cases, is determined by purely internal causes; in others external factors have a preponderating effect.

B. Growth and Cell Division

Growth, once started, does not always proceed uniformly. Some Algae such as *Vaucheria* or Fungi like *Saprolegnia* continue to extend the cell by apical growth. In the great majority of cases, however, there is a limit to this, and when a certain size has been exceeded the normal mass of the cell is regained by division. There is no regular rule, since the process depends not only on external conditions but in great part on internal. Thus, for example, divisions proceed rapidly at the growing point while they become less frequent later, though growth still proceeds. In accordance with this the size of the cells as a rule increases considerably on passing from the growing point to the region composed of permanent tissue behind. The volume of the nuclear mass is also of importance in the question of the size of the cell. It has been possible in some instances to obtain a nuclear mass twice or four times that of the normal nucleus in a cell; all the cells derived from such a cell proved to be considerably above the normal in size ([70]).

A mean volume or mass of the cell can always be regarded as one of the hereditary characters of a species. When species of different sizes are compared, the range in size of cell is not found to be as great as that in the size of the plant as a whole. In other words, large

plants are mainly (but not entirely) determined by a large number of cells ([71]).

Little is known as to the particular causes of cell division ([72]). It doubtless depends on a very complicated succession of phenomena; these concern not only the protoplasm but the nucleus which initiates the process. In the growing point of the shoot in higher plants, and also in some Algae, a certain periodicity is evident in the cell division which occurs more frequently at night than during the day; it is evident that light has an inhibiting effect, but unknown external and internal factors must co-operate. Not merely the fact that a new cell wall is formed but the direction in which it arises is a problem of developmental physiology. It has long been observed that the position of the new cell walls shows a striking similarity to the behaviour of weightless liquid films such as those of soap bubbles. The latter tend to contract to the least possible surface, and therefore are inserted as nearly as possible at right angles on the walls already present. In spite of the great similarity between the arrangement of cell walls on the one hand and of surfaces of minimal area on the other, it would be unsafe to conclude that the same causes determine the position in the two cases, for the cell wall is never fluid.

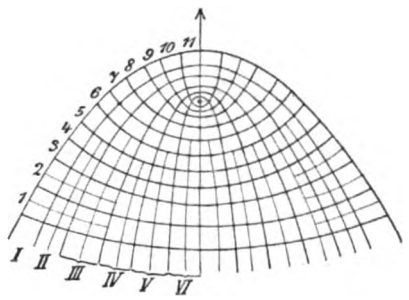


FIG. 266.—Diagrammatic representation of a growing point. (After SACHS.)

The principle of the rectangular intersection of cell walls is strikingly shown in the growing points of phanerogamic plants. In these, as is shown in SACHS' diagram (Fig. 266), the cell walls form two systems of parabolas which have a common focus and intersect at right angles. The one system (Fig. 266 *I-VI*) runs more or less parallel to the surface of the growing point; these cell walls are termed PERICLINAL. The walls at right angles to these (1-11) are termed ANTICLINAL.

C. Further Periodic Changes in Vegetative Form

Other periodic phenomena often occur while growth is active, There are, for example, periodic changes in the form of the leaves and stem, which are not only quantitative but qualitative; foliage leaves alternate with scale leaves or bracts, or leafy shoots with rhizomes. the transitions being either gradual or abrupt. The correlation of growth, already considered (p. 296), is concerned in these phenomena. The existence, or rather the activity, of a certain quantity of foliage exerts an influence on the primordia forming at the growing point

and causes them to develop as bud-scales. If the foliage leaves are removed in early summer these primordia develop as foliage leaves instead of scale leaves. In a similar fashion the removal of leafy shoots may affect a subterranean rhizome, and cause it to grow out of the soil and form foliage leaves instead of scale leaves.

Another kind of heterophylly is met with in some plants in which the form of leaves produced during youth differs from those borne on the older plant. It is sometimes possible to bring about a return to the juvenile form when the external conditions under which this arises are again established. Thus in the case of *Campanula rotundifolia* round leaves can be developed on plants which have formed the subsequent linear leaves by diminishing the intensity of the illumination. In some aquatic plants the submerged leaves belong to the juvenile form, and the floating or aerial leaves to the later adult form. Here also the juvenile form can be induced. This is not always the case, however, for sometimes the growing point has been so profoundly changed that it can only produce the later adult type of foliage.

The stem also may undergo far-reaching transformations. It may be erect in the case of leafy shoots or creep horizontally on or in the soil; in twining plants the internodes are greatly lengthened, while they are very short in rosette plants; there are wide differences in the growth in thickness, in extreme cases the stem becomes a tuber. All these various forms or modes of growth result from definite influences, and can, in part at least, be obtained experimentally even at times and places where they would not occur in the "normal" course of development.

The formation of tubers in the Potato affords an example of the plasticity of the stem. As is represented in Fig. 203, the tubers usually form at the ends of horizontal stolons which arise from the lower region of the foliage shoot where it is embedded in the soil. The tuber forms by marked growth in thickness of the end of the stolon, and cessation of its growth in length. If, however, the leafy shoot is removed at the proper time, the ends of the stolons grow into erect branches which emerge from the soil and bear foliage leaves. The typical development of the Potato can thus be modified so that no tubers are formed. On the other hand, tubers can be caused to form at other places: for example, at low temperatures the main axis of a particular kind of Potato will remain short, and be transformed into a tuber; in other varieties tubers are produced near the summit of the aerial leafy shoots when the tip of the shoot is darkened. *Boussingaultia baselloides* is even more plastic than the Potato; any bud can be induced to form a tuber, and when buds are lacking, internodes or roots may swell into tubers. Apparently the production of a certain amount of reserve material acts as a stimulus leading to the formation of a storage organ.

D. Duration of Life

We have further to consider the periodic alternation expressed in the duration of life of the plant as a whole. There are plants, such as *Stellaria media* and *Senecio vulgaris*, which in a few weeks go through their whole development from the germination of the seed to the ripening of their seeds. Since each seed can germinate at once, several generations may be developed within the year. The individual plant dies on producing a certain number of seeds, but the seeds ensure the maintenance of the type of plant. Many annual plants are similar though their life is more closely connected with the seasons of the year. With these may be placed other plants which only fruit once (monocarpic) but in which seed-formation is preceded by two or many years of purely vegetative growth, with or without resting periods. Probably in all these cases the development of fruit is the cause of the death of the vegetative organs, for their life can be considerably prolonged by preventing seed-formation. In contrast to these plants, others, such as our native trees, fruit repeatedly, the existence of the individual not being terminated by seed-formation. All perennial types exhibit another periodicity besides that due to the seasons. A tree in its first year when it is a seedling has less intensity of growth than many annual plants; the intensity of growth increases gradually and its growth in length, its growth in thickness, and even the elementary organs of the wood continue to increase in size until a maximum is attained. Some trees attain a great age and are capable of unlimited growth. From a certain point of maximum development, however, the annual shoots become smaller, apparently on account of the increased difficulty of exchange of materials between the roots and leaves. Ultimately the tree dies for this reason, or owing to the attacks of parasites or other disturbing external effects. If care is taken to ensure the production of new roots near the growing points of shoots, the latter will continue to grow with the same intensity, and no termination of the growth is to be anticipated. This experiment cannot be performed on every tree, since some do not readily give rise to roots; it is easily done with the Willow, however, by using branches as cuttings. Long before the whole individual perishes, however, single parts of it have died. Thus the leaves have been shed after persisting for one or several years. In some cases whole branches are shed, though often they perish without being thrown off and gradually break up while still attached to the plant. All the older tissues of the stem also die; the peripheral tissues are transformed into bark and either fall off or form a protective covering to the parts within. In the centre the wood is transformed into heart-wood in which the remaining living elements die. In an old tree only the growing points, whether apical or intercalary, and the youngest tissues derived

from them remain alive. Thus we see that every cell which has lost its embryonic character dies after a longer or shorter time. Though this cannot as a rule be prevented, we cannot say that the death is necessary. It is because certain cells develop that others die, and their death is a phenomenon of correlation. In plants that are capable of restitution the removal of the growing point before the permanent tissue has become too old leads to fully-grown cells, which would normally die, becoming embryonic again and continuing to live.

The longevity of trees [73] having an historical interest is naturally best known and most celebrated, although, no doubt, the age of many other trees, still living, dates back far beyond historical times. The celebrated Lime of Neustadt in Wurtemberg is nearly 700 years old. Another Lime 25·7 m. in circumference had 815 annual rings, and the age of a Yew in Braburn (Kent) which is 18 m. in circumference is estimated at 2880 years. *Sequoia gigantea*, the giant tree of California, attains according to H. MAYR the age of 4000 years. An *Adansonia* at Cape Verde, whose stem is 8-9 m. in diameter, and a Water Cypress (*Taxodium mexicanum*) near Oaxaca, Mexico, are also well-known examples of old trees. The celebrated Dragon tree of Orotava, which was overturned in a storm in 1868, and afterwards destroyed by fire, must have been some 600 years old. Bryophytes also may attain a great age; the apically-growing mosses of the calcified *Gymnostomum* clumps, and the stems of the Sphagnaceae, metre-deep in a peat-bog, must certainly continue to live for many centuries.

E. Reproduction

Cell division, especially when the two resulting cells separate, can be regarded as a process of reproduction. In more complex organisms also vegetative growth often passes gradually into reproduction. Only those forms of reproduction require special consideration in which special organs are formed (reproductive organs, germs) which separate from the parent plant and, at the expense of a supply of reserve material, commence a new life. In this way young organisms originate which then repeat the development of the parent organism, its gradual increase in strength, and its later decay. Often these reproductive organs have the further duty of carrying the organism over a period of cold or drought; they thus constitute a resting stage. With favourable conditions their growth recommences, they germinate.

Reproduction is concerned, however, not merely with the continuation of the parent organism, but at the same time with an increase in the number of individuals (p. 192). For the continuance of the species it is not only necessary that numerous germs should be produced, but that they should be widely distributed; as a rule there will be no room for new individuals to grow in the place where the plant which bears the seeds is growing.

It will be seen in the Special Part how various are the arrangements to ensure the formation of reproductive bodies in the vegetable kingdom. The division of the latter into classes, orders, etc., is mainly based on this variety. Two types of reproduction can, however, be readily recognised throughout. These are vegetative and sexual reproduction, and may also be termed monogenic and digenic respectively, since only one organism is concerned in vegetative and two in sexual reproduction.

The organs which serve for reproduction have been treated in the section on Morphology. In this place the conditions and the significance of the phenomena have to be considered and the properties of the offspring discussed.

1. The Conditions of Reproduction ([74])

In nature reproduction appears to follow vegetative growth with some degree of necessity. It commences as a rule when the vegetative growth is slackening and the plant has attained a certain age. It can, however, be shown that this succession is not obligatory, and that the natural course of development is determined by quite definite conditions, and can be greatly modified by other influences.

Thus the question arises, under what conditions does vegetative growth and under what conditions the formation of reproductive organs respectively take place? Since these problems have as yet been relatively little studied, it is not easy to give a general answer to this question. We must, therefore, confine ourselves to making clear the essential facts by means of some examples.

Lower Plants.—The fungi belonging to the genus *Saprolegnia* have a non-septate, branched mycelium without chlorophyll. They occur commonly in nature on dead insects which have fallen into water, and their thallus first grows through the body of the insect. After a time, however, it grows out and forms a radiating growth around the insect. The end of each of the radiating hyphae becomes as a rule cut off by a septum, and its contents divide up into numerous swarm-spores; these emerge, move about, and finally germinate to give rise in another place to a new individual of *Saprolegnia*. Later eggs and sperm-cells are formed on the older plant and, at least in some species, the former only develop after being fertilised. With the production of fertilised eggs the activity of the *Saprolegnia* plant tends to cease; it gradually perishes.

G. KLEBS has shown that it is possible to completely change this course of development of *Saprolegnia*; KLEBS has succeeded in directing the development in the following ways among others:

1. The mycelium can continue for the whole year to grow vegetatively when supplied continually with fresh and suitable nutritive material.

2. Such a well-nourished mycelium on being transferred to pure water proceeds completely and at once to form sporangia.

3. In solutions of leucin (0·1 per cent) and haemoglobin (0·1 per cent) at first a strong growth develops and then sexual organs are formed. Swarm-spores are not formed; they appear, however, after the sexual organs, when a more dilute solution (0·01 per cent) of haemoglobin is employed.

It is thus clear that quite definite conditions exist for vegetative growth, others for the formation of sexual organs, and yet others for the appearance of asexual reproduction.

Conditions of the Formation of Flowers.—In the Phanerogams asexual reproduction by means of bulbils, etc., is much less prominent than the sexual reproduction which is connected with the flower. The question of the causes of the development of flowers is of special interest. Observations in nature and experimental work show that in this case also sexual reproduction is not absolutely essential to the maintenance of the species, and that the formation of flowers only takes place under quite definite conditions. The results which KLEBS obtained with *Sempervivum Funkii* can be summarised thus:

1. With active carbon-assimilation in bright light and rapid absorption of water and nutrient salts, the plant continues to grow purely vegetatively.

2. With active carbon-assimilation in bright light, but with limitation of the absorption of water and salts, the development of flowers takes place.

3. With a moderate absorption of water and nutrient salts it depends on the intensity of the illumination whether vegetative growth or the production of flowers takes place. With weaker intensity of light, and when blue light is used, only growth takes place; with stronger illumination or with red light flowering occurs.

KLEBS distinguished three phases in the formation of the flowers of *Sempervivum*. 1. The establishment of the condition of readiness for flower-development. 2. The formation of the primordia of flowers recognisable under the microscope. 3. The enlargement of the inflorescence. These three phases are connected with wholly different conditions and depend therefore in different ways on external factors. The initial condition is determined by a preponderance of carbon-assimilation over processes in which carbohydrates are consumed, such as respiration and vegetative growth. Since a high temperature increases the respiration and nutrient salts promote vegetative growth, a low temperature and a limited supply of nutrient salts are necessary in addition to good illumination to render the plant ready to develop flowers. This condition when once attained may be destroyed by a high temperature, while it may be preserved for a long while, even in darkness, by a low temperature. While in this respect light

apparently acts only in determining the assimilation of CO_2, in the second phase it has another significance; a certain period of illumination is quite indispensable for this, and only the rays of greater wave-length are effective, those of short wave-length even destroying the state reached in the first phase. In nature the first phase is attained in autumn, but a sufficiently long and intensive illumination is wanting. Under continuous illumination by an Osram lamp, the light from which is rich in red rays, the formation of flowers may be hastened by months; the earlier in winter this is done the longer is the illumination required, and the period is shortened by increasing the intensity of the illumination. Interruptions in the illumination must not be too prolonged or the influence of the illuminated period is lost. The third phase of elongation is, like the first, dependent on the nutritive effect of light; in accordance with this, if the preceding nutrition has been sufficient it may, in part at least, be carried out in the dark.

Similar thorough analyses of the conditions of flowering are not available as yet for other cases, but numerous observations and experiments indicate that light, temperature, and the nutrient salts are of primary importance in the formation of the flowers. Since these factors are also indispensable for the vegetative life of the plant, it is the amount in which they are available and especially their relative proportions which determine whether a particular bud shall form a flower or grow vegetatively.

The importance of light in the formation of flowers is shown by the well-known fact that the Ivy only flowers when growing in a well-illuminated situation and not in the shade of woods, although it grows well in the latter habitat. VOECHTING'S experiments on *Mimulus Tilingii* gave the same result. At a certain low intensity of light, which is quite adequate for vegetative growth, this plant produces no flowers. KLEBS has made corresponding experiments with *Veronica Chamaedrys*, and he states that in all plants which do not contain any great amount of reserve materials a diminution of light leads to the suppression of flower-formation. He regards the carbon-assimilation resulting from the illumination as the primary cause of this influence on the development of flowers. At a certain intensity of light, which is insufficient for the development of normal flowers, cleistogamous flowers are produced.

Temperature also obviously plays a part. A continuous high temperature hinders flowering. Thus plants of our climate eventually become vegetative in the tropics (Cherry), and native perennial plants, such as the Beet or Foxglove, can be prevented from flowering in their second year if they are kept warm and allowed to grow on during the winter. In this way KLEBS succeeded in keeping the Beet in a purely vegetative state for several years. *Glechoma* and *Sempervivum* also, if their winter rest is prevented, grow vegetatively for years.

Lastly, the nutrient salts have to be considered. By removing the supply of salts, seedlings can often be converted into dwarf starved plants in which, after a few minute foliage leaves have been formed, the development of flowers begins at once. Experiments of MOEBIUS have shown that Grasses and *Borago* flower better if the supply of salts is limited than if well manured. The increase of fertility which results from root-pruning in fruit trees may depend upon a limitation of the absorption of nutrient salts. That, however, all nutrient salts do not act in the same way has been pointed out by BENECKE, who showed both from the literature

and from his own experiments that nitrogenous food led to a diminution and phosphorus to an increase in the development of flowers.

If after the formation of flowers has commenced the conditions for vegetative growth are re-established, a shoot already predisposed to flower-formation may again become vegetative. Thus when *Mimulus Tilingii* is brought into conditions of poor illumination the flower-buds already laid down remain undeveloped and resting buds in the axils of bracts develop into leafy shoots. The whole appearance of the plant is thus greatly altered.

Determination of Sex (75).—Most flowers are hermaphrodite and produce both male and female sexual cells. In other cases unisexual flowers are produced either only or in addition to the hermaphrodite flowers. The fact that the female flowers are developed as a rule in different situations from the male flowers indicates that each of the two forms has its special conditions of development; what these conditions are is, however, unknown.

The determination of sex thus becomes a problem of developmental physiology especially when dioecious plants (*i.e.* those which have male and female individuals) are concerned. Generally the two forms occur in about equal proportions in nature, and this relation cannot be altered experimentally. It is also not possible by means of external influences of any sort to cause a seed to develop into the one or other sexual form. The sex is already determined in the seed as a result of internal causes which will not be further considered here; these have already acted in the sexual cells or at fertilisation.

Fertilisation.—The product of fusion of the egg and sperm-cell surrounds itself, as a rule, with a cell wall. In the lower plants an oospore or zygospore is thus formed which germinates, usually after first undergoing a period of rest. In the higher plants growth and cell division take place forthwith; an embryo is produced which in Bryophyta and Pteridophyta continues its further development, while in the Phanerogams it soon enters on a period of rest. Before this, however, a number of stimuli have proceeded from the development of the embryo; these are especially complex in the Angiosperms. The ovule in which the embryo is enclosed commences to grow; it enlarges and assumes a characteristic structure. It has developed into the seed, and this as a rule is liberated from the ovary and, after a resting period, germinates. The ovary also grows actively after fertilisation and develops into the fruit. The variety in fruits cannot be entered upon in this place. (Cf. Special Part.)

These formative processes of growth in the ovules, ovary, and ultimately also in other parts of the flower, are to be regarded as phenomena of correlation. When fertilisation does not take place, all those changes which lead to the development of a ripe fruit from the flower do not usually occur. Instead another correlative influence arises which leads to the casting off of the now useless organ as a whole. Some few plants, especially such as have been long cultivated, are to some extent an exception to this. In nearly all varieties of the Banana, in the seedless Orange, and in the Sultana Raisin, no embryo is formed, but in spite of this the fruits develop. The stimulus to this development can proceed either from the mere pollination of the stigma or from the fertilisation of the ovules, which then sooner or later cease to develop without arresting the development of the fruit. In some

cases, however, "barren" fruits develop wholly without the stimulus of pollination (parthenocarpic [76] fruits of the Fig, Cucumber, and certain species of Apple and Pear).

Influences which affect parts at a distance also proceed from the pollen-grains and pollen-tubes on the stigma. Thus after the stigma of an orchid is pollinated the stigma and the gynostemium swell, and the perianth is promptly arrested in its growth and withers. As FITTING [77] showed, this influence proceeds from soluble organic substances which withstand heating, and can be readily separated from the mass of ungerminated pollen.

Whether a simple spore or a complex embryo is the result of fertilisation it is always distinguished from the cells which gave rise to it by exhibiting nuclei which contain the diploid number of chromosomes (p. 203). On this account a reduction division which restores the normal number of chromosomes is sooner or later the necessary sequel to fertilisation.

2. The Significance of Sexual Reproduction

The significance of sexual reproduction is not at once evident. Many plants occur in nature or under cultivation without being sexually reproduced, and succeed with vegetative reproduction only.

Lower plants which have not attained to sexual reproduction have already been referred to. Of higher plants which no longer produce descendants sexually the cultivated Bananas, some Dioscoreaceae, some forms of Vine, Oranges, and Strawberry may be mentioned. The Garlic, which forms small bulbils in place of flowers, the White Lily, and *Ranunculus Ficaria*, which has root-tubers, only rarely produce fertile seeds if allowed to form their vegetative organs of reproduction. Under certain conditions, as for instance on cut inflorescences, seeds may be produced, though as a rule these plants are multiplied entirely vegetatively. No degeneration such as was formerly held to be unavoidably associated with purely vegetative multiplication is to be observed in these cases [78].

If thus the monogenic reproduction suffices to maintain the species digenic reproduction must serve some further purpose not effected by the former. Otherwise it would be inconceivable why digenic reproduction had arisen, and why the arrangements to effect it are far more complicated and less certain than in the case of vegetative reproduction.

Were the Algae and Fungi alone taken into consideration it might be supposed that sexual reproduction led to the formation of specially resistant germs which could endure a longer period of rest under unfavourable conditions—as a matter of fact the zygospores and oospores are much more resistant than the swarm-spores and conidia. But even in the Pteridophyta this relation is inverted, for the fertilised egg-cell requires to develop forthwith, or else it perishes, while the asexual spores can endure a long resting period.

It is the rule in digenic reproduction that the sexual cells are individually incapable of development; this takes place only after the sexual cells have united. Thus one use of fertilisation lies in the

removal of an arrest of growth, though it cannot be said that this was its original and essential significance. It is much more probable that the sexual cells have gradually lost the capacity of independent development since in this way the possibility of fusion was increased. If every sexual cell commenced to grow at once, this would in most cases take place before fusion with another sexual cell could be effected

This assumption is supported by the behaviour of some Algae, in which the sexual cells can often germinate independently; the egg-cells especially may develop without fertilisation. From the analogy with similar cases in the animal kingdom this phenomenon has been termed PARTHENOGENESIS. In the primitive Algae parthenogenesis is possible, because in them the incapacity of development of the egg-cell has either not been acquired or is easily removed under special conditions. Thus for example in the Alga *Protosiphon* parthenogenetic development is induced by a high temperature, and the same happens in the case of the ova of some lower animals (Echinoderms) on treatment with solutions of a certain concentration. It may perhaps be assumed that in the cases in which development only takes place after fertilisation the stimulus to development is given by some substance contained in the sperm-cell.

Among the higher plants also phenomena to which the name parthenogenesis ([79]) has been applied occur; they are better termed apogamy. Thus the egg-cells of some Compositae, and also of *Alchemilla*, *Thalictrum purpurascens*, *Wickstroemia indica*, *Ficus hirta*, *Marsilia Drummondii*, and *Chara crinita* develop without previous fertilisation. These cases are distinguished from those just described by the egg-cells in question having retained the number of chromosomes characteristic of vegetative cells. They are diploid cells (p. 203) and not fitted for fertilisation.

We thus arrive at the conclusion that the essential of sexual reproduction cannot consist in the removal of the arrest to development of the sexual cells. This leads us to consider THE FUSION OF THE SUBSTANCE OF THE TWO CELLS AND THE MINGLING OF PATERNAL AND MATERNAL CHARACTERS WHICH FOLLOWS FROM THIS. This brings out the chief distinction between the two modes of reproduction; the vegetatively produced progeny are due to no such mingling of characters. The complex of characters in vegetative multiplication does not differ as a rule from that in the parent form. As a matter of fact, we preserve by vegetative multiplication all the varieties and races of our cultivated plants, even when these do not come true from sexually produced seed. In contrast to the vegetative progeny the sexually produced descendants, as a rule, cannot completely resemble the mother plant, but must combine the characters of both parents. The more these differ from each other, the more striking will be the visible effect of fertilisation.

F. Heredity, Variability, Origin of Species

Heredity ([80]).—By inheritance is understood the familiar phenomenon that the properties of the parents are repeated in their progeny. This phenomenon is presented to us in the division of a

cell, which is the simplest form of reproduction, as well as in the more complicated process of sexual reproduction. That the daughter cells resemble the parent cells requires no explanation. The problem of heredity appears when descendants are derived from the GERMS, which are small portions of a complicated parent organism, by a process of DEVELOPMENT. It is assumed that such germs possess DETERMINANTS or GENES, which determine that an organism shall react in a definite specific way to external factors. It appears probable that these determinants are associated in the chromosomes of the nucleus, but we know nothing as to the way in which they influence the course of development.

Such determinants must be present in the sexual cells of the higher plants, and both in the male and the female cells. The fertilised egg-cell must thus possess a double number of these though a single organism is derived from it. That, originally at least, the same determinants are present in all cells of the plant and not only in the germ cells is shown by the phenomena of restitution.

The problems of inheritance are of greatest interest in sexual reproduction, in which the part played by the two parents in the organisation of the progeny comes into prominence. These problems can only be attacked by a consideration of hybrids, since the individuals of a pure species have the same determinants.

Hybrids ([81]).—The union of two sexual cells is, as a rule, only possible when they are derived from individuals of the same species; it is only then that they fuse together in the act of sexual reproduction. Occasionally, however, the sexual cells of different varieties, species, or even genera have been shown to be able to unite and produce descendants capable of development. Such a union is termed HYBRIDISATION, and its products HYBRIDS. They are also spoken of as HETEROZYGOTES or individuals derived from two dissimilar sexual cells, in contrast to HOMOZYGOTES, which have arisen from the union of sexual cells with identical determinants. Hybrids are as a rule obtained more readily the closer the parent forms are to one another, but this is not a rule without exceptions.

Some families exhibit a tendency to hybridisation (Solanaceae, Caryophyllaceae, Iridaceae, etc.) while in others hybrids are obtained with difficulty or not at all (Papilionaceae, Coniferae, Convolvulaceae, etc.). The behaviour of related genera and species also is frequently very different. Thus species of *Dianthus*, *Nicotiana*, *Verbascum*, and *Geum* readily hybridise with one another, while those of *Silene*, *Solanum*, *Linaria*, and *Potentilla* are difficult to hybridise. Hybridisation of closely related species may frequently fail when more distant species can be crossed.

Hybrids also occur in nature, especially in the genera *Salix*, *Rubus*, *Hieracium*, and *Cirsium*. That such natural hybrids do not occur oftener is due to the lack of an opportune time or space for their development, and also to the fact that in the case of pollination of flowers with different kinds of pollen, that of their own species seems as a rule more effectual in effecting fertilisation.

FIG. 267.—1. *Sorbus aucuparia*. 2. *Sorbus aria*. 3. The hybrid between these.
(After SCHLECHTENDAL, LANGETHAL and SCHENK. *Flora v. Deutschland*, 5th ed. by HALLIER.)

Hybrids are often recognisable by having the characters of intermediate forms between the two parents. They may either be truly intermediate, *e.g.* *Nicotiana rustica* ♀ × *Nic. paniculata* ♂ and *Sorbus aria* × *S. aucuparia* (Fig. 267), or may in some characters resemble more closely the male parent and in others the female parent. In exceptional cases a hybrid may, even to minute characters, resemble the male parent (some hybrids of the Strawberry) or the female parent. In the great majority of cases it is all the same which plant is taken as the male and which as the female parent. In some cases, however, the hybrid A ♀ × B ♂ is clearly different from A ♂ × B ♀.

The mingling of characters is often complete. Had one species simple and the other compound leaves, their hybrid would have leaves more or less cleft (Fig. 267); or were the flowers of one parent species red and those of the other yellow, the hybrid frequently bore flowers which were orange-coloured. If an early blooming form were crossed with a late bloomer, the hybrid would flower at a time intermediate between the two. Another type of hybrid which is less commonly met with is that of the MOSAIC HYBRIDS. In this parts with maternal characters are mingled with others which have the characters of the male parent.

New characters appear in hybrids such as diminished fertility, a greater tendency to the formation of varieties, and frequently a more luxuriant growth.

The fertility is often so enfeebled that the hybrids either do not flower (*Rhododendron*, *Epilobium*), or are sterile and do not reproduce themselves sexually. This enfeeblement of the sexuality increases the more remote is the relationship of the ancestral forms. Other hybrids such as those of *Salix* and *Hieracium* remain fertile.

Hybrids, particularly those from nearly related parents, frequently produce more vigorous vegetative organs, they bloom earlier, longer, and more profusely than the uncrossed plants, while at the same time the flowers are larger, more brilliant, and exhibit a tendency to become double. The luxuriance of growth and the increased tendency to produce varieties displayed by the hybrids have made the whole subject of hybridisation one of great practical as well as theoretical importance.

Inheritance in Hybrids (82).—By the experimental study of hybridisation, the sexuality of plants, for a long time doubted, was indisputably proven. With this object in view, hybrids were raised in great numbers by KÖLREUTER as early as 1761. It is now the problems of inheritance connected with hybridisation that are the main centres of interest. For the study of heredity, however, hybrids between species are far too complicated. It was by using closely related forms that GREGOR MENDEL at Brünn discovered in 1866 certain laws, which, however, did not attract attention or influence the progress of investigation till after 1900. At this date they were re-discovered simultaneously by DE VRIES, CORRENS, and TSCHERMAK. In order to obtain these laws or rules MENDEL required to follow the behaviour of the hybrids through a number of

recently shown that, at least in a particular stage of development, the homozygous plants of *Urtica pilulifera* can be distinguished from the heterozygotes. Nevertheless it may be said that two plants possessing different determinants may be apparently similar, while on the other hand two organisms possessing the same determinants may appear distinct owing to diverse action of the environment. The nature of the determinants which are contained in a plant can thus not be discerned from its appearance but only by breeding experiments.

3. AUTONOMY OF CHARACTERS.—When the parents differ in two characters instead of only one, monohybrids instead of dihybrids result. It then appears that the several characters are independently transmitted and distributed in the descendants (autonomy of characters). Thus new combinations of characters may come about, a fact of great importance in plant-breeding. From the crossing of peas with yellow, wrinkled seeds, and those with green, smooth seeds, among other possible combinations of the characters the new ones yellow-smooth and green-wrinkled appear. Many characters, however, tend to remain associated together (coupled characters).

It is not possible to enter in this place into the complicated phenomena of the production and segregation of dihybrids and polyhybrids.

Validity of the Mendelian Rules.—These rules are not limited to hybrids in the narrow sense of the word, but have an extensive application to inheritance in both the animal and vegetable kingdoms. It cannot be said that there are not other laws followed in inheritance, for there are already well-investigated cases which do not conform to the Mendelian rules (84). On the other hand, it is noteworthy that many phenomena which at first appeared to contradict these rules have proved on further investigation to be consistent with them.

Variability (85).—By variability is understood the fact that the individuals belonging to any species are not all alike. Frequently the variability is only apparent, the species not having been properly defined. Thus in *Rosa*, *Rubus*, *Draba verna*, etc., there are many species that closely resemble one another. The impression given of a "varying" species is in these cases a completely false one; each of the "ELEMENTARY SPECIES," of which the "COLLECTIVE SPECIES" is composed, proves to be constant and does not exhibit transitions to the other elementary species.

Such cases are to be left out of consideration here. We are concerned with the most strictly limited species, if possible with the descendants of a single self-fertilised plant constituting what is known as a pure line (JOHANNSEN). It is found that these also vary. The process of variation and the varieties can be traced to two causes and are therefore distinguished as MODIFICATIONS and MUTATIONS. To these must be added the combinations originating from crossing.

MODIFICATIONS.—This name is given to variations which have

gated into pure red and pure white sexual elements. In the process of fertilisation the union producing a hybrid, red × white (white ♀ × red ♂, red ♀ × white ♂), will occur twice as frequently as the union red × red or white × white, which give rise to pure forms.

2. RULE OF DOMINANCE.—The characters in which the parents differ do not, however, always blend so that the hybrid exhibits an intermediate character. More usually the hybrids completely resemble in this respect either the paternal or maternal parent, the character of the one parent being dominant in the hybrid while the

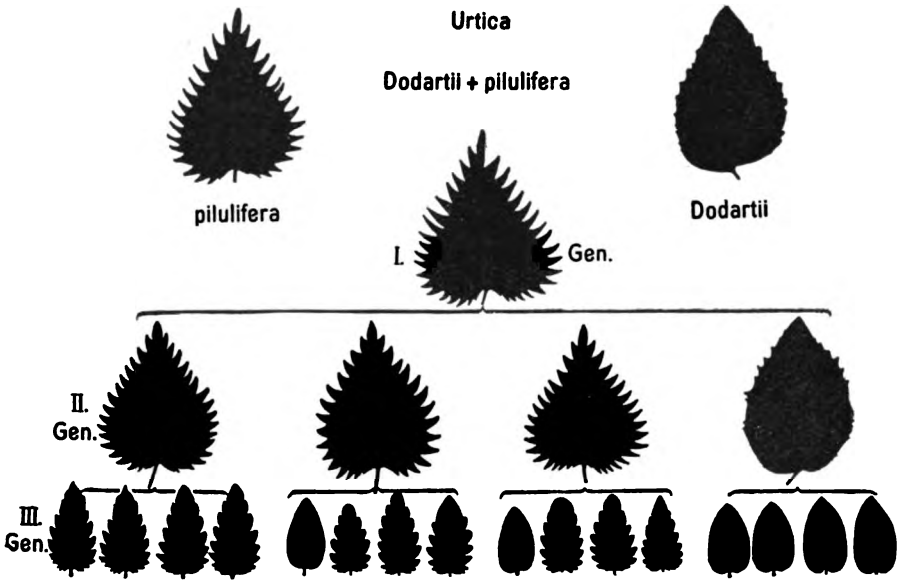


FIG. 269.—The hybrid between *Urtica pilulifera* and *Urtica Dodartii* in three generations. (Diagram. After CORRENS.)

other remains latent. This is the case, for example, in hybrids between *Urtica pilulifera* with serrate leaves and *U. Dodartii* (Fig. 269). The hybrids have all serrate leaves like *U. pilulifera*, so that in the second generation the proportion of serrate-leaved to entire-leaved individuals is per cent 75 : 25 (3 : 1). Only 50 per cent of the serrate-leaved individuals are, however, of hybrid nature and continue to show a similar splitting of characters in the next generation; 25 per cent have become pure *U. pilulifera*. It is impossible to predict which characters will prevail in any cross, and the question can only be settled by experiment; usually the phylogenetically younger character appears to be dominant.

With regard to the above example of dominance CORRENS [83] has

grow two plants of the same origin under completely identical conditions they would necessarily be indistinguishable. In practice this is never possible, and therefore the homozygotic individuals of a pure line show many quantitative differences even under the most uniform cultivation possible. For example, the seeds of a pure line of Bean can be sorted into a number of groups according to their weights, and the number in each group or category ascertained. The result of such an investigation is the curve in Fig. 271, which shows that the weight-categories that occur most frequently are those closest to the average weight, and that the farther a category is from the average the fewer are the individuals belonging to it. Practically all statistical investigations of variation conform to this result. The VARIATION CURVES thus obtained agree more or less closely with the so-called curve of chance. This is readily understood, for there are always several external factors acting which may result in either an increase or diminution of the size, number, or weight under consideration. Only chance decides which effect takes place. Thus only rarely will all the factors make for diminution or all the factors for increase; more frequently the factors will be combined so as to determine an intermediate result.

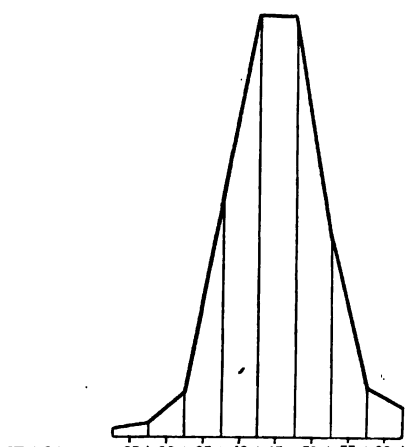


FIG. 271.—Variation curve of the weights of Beans of a pure line (JOHANNSEN'S Line K). (After BAUR.)

If a seed of a pure line is sown it is indifferent whether one starts from a small, medium, or large specimen. The variation curve of the next generation will not differ from that of the generation to which the seed belonged. Similarly the changes resulting from cultivation in alpine regions (Fig. 270) are not inherited. Such modifications persist only as long as, or but little longer than, the action of the causes giving rise to them.

Practical experience seems at first sight to contradict this result. In the process of SELECTION a plant with special properties is chosen from a large number and the same characters appear to recur frequently in its descendants. This depends on the fact that in this case a single pure line has been isolated from what was really a mixture of a number of different races or lines. The characteristic properties of the selected line are continued in the

descendants. If the material to begin with is really pure, selection has no effect.

COMBINATIONS.—When a plant originates not from self-fertilisation but from a cross, this may be termed a hybrid even if its parents belonged to very nearly related races. In this sense in every cross between two individuals heterozygotes must appear. The descendants of a hybrid will have the characters of the one parent or of the other or of both, and will thus appear diverse. This form of variation is superficially not to be distinguished from modification, for it can also show the curve of chance. It is, however, essentially different since it is inheritable. The descendants vary according to the Mendelian rules. This form of variation is termed combination.

FIG. 272.—Habit of *1*, *Chelidonium majus*; *2*, *Chelidonium majus laciniatum*. (After LEHMANN.)

MUTATIONS (86) are variations that are distinguished from combinations in not having arisen by hybridisation, but resemble them in being inherited. Mutations can only be recognised with certainty under experimental conditions, when in the descendants of a pure line individuals appear which possess a new character or are wanting in a character of the parent organism, the departure being maintained in their offspring. The appearance of such mutations has been observed in experiments both with seedlings and with buds. It is also highly probable that many variations met with in nature should be regarded as mutations. Thus, for example, *Chelidonium laciniatum*, a mutation of *Chelidonium majus* with incised leaves, was found at Heidelberg in 1590 (Fig. 272). *Fragraria monophylla*, which was first noticed in 1761, differs from the ancestral form of the Strawberry in having simple instead of trifoliate leaves. The remarkable

Nicotiana tabacum virginica apetala, which arose in a culture of KLEBS, must be placed here. In many plants reddish-leaved forms have arisen as mutations. All these forms are distinguished from the parent form in a single character. Once they have arisen they have remained constant in all their descendants.

Nothing certain is known as to the causes of mutations. If they should prove in certain cases to be determined by external factors they would still be sharply distinguished from modifications. In the mutation a change in the determinants has occurred; either old determinants have been lost or new ones have made their appearance. The latter case must, however, be rare. Mutations do not appear only in relation to sexual reproduction. Thus in some Bacteria which increase in number by repeated division mutations have been found. In higher plants also single buds are known to have become changed and their new characters have persisted. These cases are spoken of as bud mutations. Doubt is often expressed as to whether in the Bacteria and in the moulds there is any sharp distinction between mutations and modifications.

Origin of Species.—Various lines of evidence, dealt with on p. 206 ff., have led to the view that the organisms which inhabit the earth at the present time have developed from others that existed in previous ages. This hypothesis, which is known as the THEORY OF DESCENT (87) and is of great importance, assumes that the "species" is not constant but liable to change. In addition to what has been said earlier (p. 206 ff.) it is only necessary to state here that only mutations and combinations among the variations yet observed could play a part in the origin of a new species. Latterly the indications that hybridisation has been of importance in the production of species have multiplied. Certain species of *Oenothera* behave like hybrids the parents of which are no longer in existence.

SECTION III

MOVEMENT

Phenomena of movement are met with in the living plant not less generally than those of metabolism and development. Metabolism is associated with a continual movement of the raw food-materials, which are absorbed, and of the elaborated assimilates and excreted substances. These movements cannot be directly observed, but are not less certainly established; they have already been dealt with. In addition there exist a number of visible alterations of position exhibited either by the whole plant or by its several organs; these movements are, it is true, often very slow but sometimes are quite sudden.

PROTOPLASM itself is capable of different movements. Naked protoplasmic bodies almost always show slow movements resulting in

a gradual change of position; but cells enclosed by cell walls possess also the power of INDEPENDENT LOCOMOTION, often indeed to a considerable extent. Multicellular plants, however, as a rule ultimately attach themselves, by means of roots or other organs, to the place of germination, and so lose for ever their power of locomotion, except in so far as it results from growth.

Many perennial plants do not reappear in exactly the same spot. Since new parts arise by growth while old portions die off, such plants change their place gradually. A good example is afforded by plants with rhizomes growing forward at the tip while the hinder region is decaying. In trees the main axis continues alive, but the growing points are changing their position; thus the growing point of a giant Australian *Eucalyptus* moves from the level of the soil to a height of 110 m.

Geophytes (p. 177) moving forward in a straight line in the ground come to new places, the food materials of which have not been used up by them. This movement is especially evident in those in which the rhizome remains short, owing to the former year's growth soon decaying. The annual movement in *Listera ovata* is only 3-5 mm., in *Arum maculatum* 1-3 cm., and in *Paris quadrifolia* 6-8 cm. The change of place is more marked in the case of plants provided with special off-shoots or runners. The movement is not really wanting in geophilous plants which continue in the same spot (Ophrydeae), because the direction of elongation regularly alternates, or as in *Colchicum* because the new shoots in their expansion have to force their way through the remains of the previous year's growth. In the latter case the corms may be laterally distant, 5-7 cm., from the foliage leaves and connected with these by means of an S-shaped curved stem.

In addition to these movements, occasioned by a growth in length, plants firmly established in the soil also possess the power of changing the position and direction of their organs by means of CURVATURE. Not only unequal growth but other processes also take part in these changes of form. In this way the organs are brought into positions necessary or advantageous for the performance of their functions. By this means, for example, the stems are directed upwards, the roots downwards; the upper sides of the leaves turned towards the light, climbing plants and tendrils twined about a support, and the stems of seedlings so curved that they break through the soil without injury to the young leaves.

Movements of locomotion and movements of curvature have thus to be distinguished.

I. MOVEMENTS OF LOCOMOTION ([88])

A. Mechanism of Movements of Locomotion

In a fuller consideration of changes of position we can leave on one side the carriage forward in a straight line by means of growth of the growing point, since this has been dealt with in the chapter on

development. We thus confine ourselves to the protoplasmic movements among which the AMOEBOID MOVEMENT, the CILIARY MOVEMENT, and the MOVEMENT OF PROTOPLASM IN CELLS WITH CELL WALLS may be distinguished.

The creeping movements of naked protoplasts, such as are shown by an amoeba or plasmodium, in the protrusion, from one or more sides, of protuberances which ultimately draw after them the whole protoplasmic body, or are themselves again drawn in, are distinguished as AMOEBOID MOVEMENTS. These movements resemble, externally, the motion of a drop of some viscous fluid on a surface to which it does not adhere, and are chiefly due to surface tension, which the protoplasm can at different points increase or diminish by means of its quality of irritability.

By means of local changes of surface-tension similar amoeboid movements are also exhibited by drops of lifeless fluids, such as drops of oil in soap solution, drops of an oily emulsion in water, or drops of mercury in 20 per cent solution of potassium nitrate in contact with crystals of potassium bichromate.

In the SWIMMING MOVEMENTS BY MEANS OF CILIA ([89]), on the contrary, the whole protoplasmic body is not involved, but it possesses special organs of motion in the form of whip-like FLAGELLA or CILIA. These may be one, two, four, or more in number, and arranged in various ways (Figs. 216, 219). They extend through the cell wall when this is present and move very rapidly in the water, imparting considerable velocity to the protoplast, often giving it at the same time a rotary movement. The minute swarm-spores of *Fuligo varians* traverse 1 mm. (sixty times their own length) in a second, those of *Ulva* 0·15 mm., while others move more slowly. The *Vibrio* of Cholera, one of the most rapidly moving bacteria, takes 22 seconds to traverse a millimetre.

Diatoms and Desmids exhibit a different class of movements. The Diatoms which have a slit or raphe in the siliceous cell wall glide along, usually in a line with their longitudinal axis, and change the direction of their movements by oscillatory motions. From the manner in which small particles in their neighbourhood are set in motion, it is concluded that there exists a current of protoplasm, which bursts through the raphe; this, according to O. MÜLLER, is the cause of the movement ([90]). The cells of Desmidiaceae effect their peculiar movements by local fluctuations in the mucilaginous excretion. The Oscillarieae appear to behave similarly ([91]).

In addition to such changes of place of whole cells there are also movements of the protoplasm within the cell wall. Of these movements rotation and circulation (cf. p. 13) have to be distinguished.

In these movements the outermost layer of protoplasm in contact with the cell wall remains at rest; the movement cannot thus be compared to that of an amoeba enclosed in a cell. The movement continues when the protoplasm has been detached from the cell wall. Its cause must be looked for in surface tensions between the protoplasm and the cell sap.

The streaming movements of protoplasm were discovered by CORTI in 1772. Favourable examples for their demonstration are the hairs of many plants, the cells of the leaves of some water plants, and the long cells of the Characeae and Siphoneae.

B. The Conditions of Locomotion

Since these movements are due to protoplasm and its organs it will be readily understood that they depend on the general conditions for the life of the protoplasm.

The existence and the activity of all these movements thus depend especially on a favourable temperature, and in aerobic plants on the presence of free oxygen. The protoplasmic movement can, however, continue for weeks in the absence of oxygen in the case of facultative anaerobes like *Nitella*. Certain Bacteria that are obligate anaerobes lose their motility on the entrance of oxygen; on the other hand, aerobic Bacteria which have ceased to move in the absence of oxygen resume their movement when a supply of this gas is available (p. 248).

On overstepping the minimum or the maximum for these factors a loss of motility or a condition of rigor results. Thus we speak of cold-rigor, heat-rigor, etc. This condition can be removed by a return of the favourable conditions, but if it lasts long enough will ultimately lead to death. In some cases it is sufficient that these general conditions of life should be present, but in others the movement only results on the application of a special stimulus.

Thus it is known that protoplasmic movement often only appears on wounding the plant, or is increased by this. In certain Bacteria movement is started by the stimulus of light or by a particular concentration of the substratum. Other external influences may lead to a loss of motility, while movement also ceases in temporarily motile objects, such as swarm-spores or spermatozoids, as the result of internal causes.

In giving a definite direction to movements of locomotion, external stimuli play a very special part. In the absence of such directive stimuli plasmodia move without a destination, the direction of swimming or circulatory movements may frequently be reversed, and only the rotation-stream is characterised by a constant direction.

C. Tactic Movements

The main directive stimuli are one-sided illumination, and dissolved substances unequally distributed through the water. The directive movements brought about by such factors are termed tactic; that effected by light is phototaxis, and that by dissolved substances chemotaxis. Other less widespread tactic movements will be omitted here.

The resulting movements bring the freely motile plant or the motile organ of a cell either towards or away from the stimulus; in

the former case the taxis is positive, and in the latter negative. The nature of the reaction frequently depends not only on the object, but on the external conditions.

1. Phototaxis (92)

Phototactic movements may be best observed when a glass vessel containing water in which are Volvocineae, Chlamydomonadinae, or swarm-spores of Algae is exposed to one-sided illumination from a window. After a short time the uniform green tint of the water disappears, since the motile organisms have all accumulated at the better-illuminated side of the vessel. If the latter is turned through an angle of 180° the Algae hasten to the side which is now illuminated. If, however, a stronger light, such as direct sunlight, is allowed to fall on the vessel the same organisms which till now have reacted positively become negatively phototactic and swim away from the source of light. Other external factors may have the same effect.

In some organisms, such as the plasmodia of Myxomycetes, we find a negative reaction even to a light of low intensity. There are also colourless organisms which have a positive phototactic reaction. In nature phototactic movements usually bring the organism into a position of optimal illumination.

There are two distinct kinds of phototaxis. In the one (TOPOPHOTOTAXIS) the organism places itself in the direction of the rays of light, and moves towards or away from the source of light. In other cases (PHOBOPHOTOTAXIS) the organism reacts on the passage from light to darkness by a sudden movement that brings it back into the light; it thus remains fixed in the illuminated spot.

A very striking example of phototaxis is afforded by the chloroplasts within the cell (93). These movements have the result of bringing the chlorophyll grain into such a position that it can obtain an optimal amount of light. This object is sometimes attained by rotation of the chloroplast, and sometimes by its movement to another position in the cell.

In the cylindrical cells of the filamentous Alga *Mesocarpus*, the chloroplasts, in the form of a single plate suspended length-wise in each cell, turn upon their longitudinal axes according to the direction and intensity of the light. In light of moderate intensity they place themselves transversely to the source of light, so that they are fully illuminated (transverse position); when, on the other hand, they are exposed to direct sunlight, the chlorophyll plates are so turned that their edges are directed towards the source of light (profile position).

In the leaves of mosses and of the higher plants and in fern prothalli a similar protection of the chloroplasts against too intense light, and their direct exposure, on the other hand, to moderate illumination, is accomplished, where they are of a different form and more numerous, by their different disposition relatively to the cell walls. In moderate light the chlorophyll bodies are crowded along the walls, which are at right angles to the direction of the rays of light (Fig. 273 *T*). They, however, quickly pass over to the walls parallel to the rays of light as soon as the light becomes too intense, and so retreat as far as possible from its action (Fig. 273 *S*).

In darkness or in weak light the chloroplasts group themselves in still a third way (Fig. 273 *N*), the advantage of which is not altogether clear.

The form of the chlorophyll grains themselves undergoes modification during changes in their illumination; in moderate light they become flattened, while in light of greater intensity they are smaller and thicker. As a special mode of protection against too intense light, the chloroplasts of the Siphoneae and Diatomeae (and the same thing is observed in many plants) become balled together in separate clumps.

In correspondence with the changes in the position of the chloroplasts, the colouring of green organs naturally becomes modified. In direct sunshine they appear lighter, in diffused light a darker green.

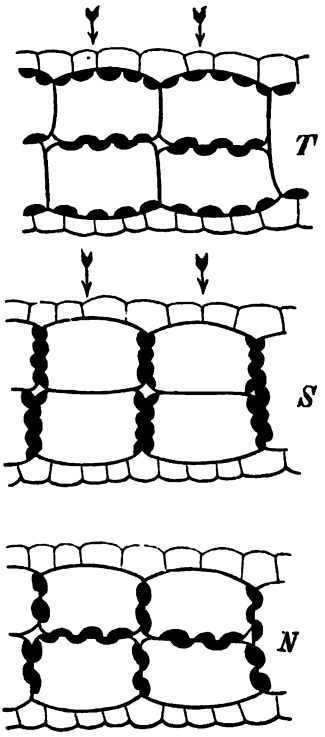


FIG. 273.—Varying positions taken by the chlorophyll grains in the cells of *Lemna trisulca* in illumination of different intensity. *T*, in diffuse daylight; *S*, in direct sunlight; *N*, at night. The arrows indicate the direction of the light. (After STAHL.)

2. Chemotaxis (94)

Chemotaxis results, as mentioned above, from the unequal distribution of substances dissolved in water. Positive chemotaxis leads to the irritable plants accumulating in the region of higher concentration of the chemotactic material.

Such substances are of definite nature. Thus, for example, many bacteria are "attracted" by particular organic or inorganic food materials, *e.g.* peptone, sugar, meat-extract, phosphates, etc., while they are "repelled" by other substances such as acids and alkalies. While the chemotaxis here serves the process of nutrition, its use is different in the case of spermatozoids; these male sexual cells are thus attracted to the egg-cells. Nuclei and chloroplasts may also show chemotactic movements.

The spermatozoids of the Ferns are attracted by malic acid or malates to the neck of the archegonium; in the case of the spermatozoids of Lycopodium, citric acid, in Mosses, cane sugar solution, and in the Marchantieae proteid substances are the respective attractive substances. Often extremely minute quantities of the substance will bring about active irritable movements; thus even a 0·001 per cent solution of malic acid will attract the numerous spermatozoids of a Fern swimming in pure water. In chemotaxis as in phototaxis we can distinguish phobic and topic modes of reaction.

Aerotaxis determined by oxygen is found in the case of Bacteria;

on this account these organisms have been used to demonstrate the assimilation of carbon dioxide (p. 248).

The phenomenon of hydrotaxis, a directive movement due to the unequal distribution of water-vapour in the air, may be associated with chemotaxis. A positive hydrotaxis is shown by the plasmodia of Myxomycetes, and this passes into negative hydrotaxis at the time of spore-formation.

II. MOVEMENTS OF CURVATURE

The **kinds of curvature** which may take place in the organs of attached plants are illustrated by Fig. 274. A four-angled prism is of equal length along each of its angles. If it is bent in one plane the angles of the concave side must become markedly shorter than those of the convex side. An elongation of one side or a shortening of the other side or simultaneous lengthening of one side and shortening of the opposite side must lead to curvature. When in this process of bending the column remains in one plane, it is spoken of simply as curved. When, however, it passes out of the one plane so that the bending follows a line oblique to the longitudinal axis it is spirally wound (*IV*). Lastly, when the column remains as a whole straight but its angles follow spiral lines, it is termed twisted (III). The torsion comes about by a difference in length between the middle line and the angles; all the latter are of equal length.

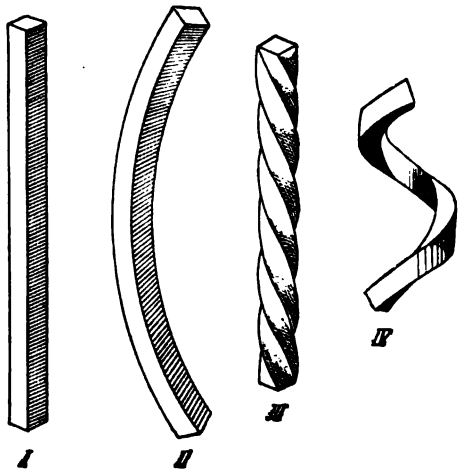


FIG. 274.—Four-angled prism. *I*, Straight; *II*, curved; *III*, twisted; *IV*, spirally wound.

Ways in which Curvatures are produced.—In the production of curvatures we are always concerned, as has just been shown, with changes in the dimensions of an organ due to unequal lengthening or shortening. In bringing about these changes in dimension the following means are employed by the plant.

1. Growth. This can only lead to elongation.
2. Osmotic pressure. This can effect an elongation or a shortening according as it is increased or diminished.
3. Variations in the amount of water in the cell wall or in dead cells. These also can effect either elongation or shortening.

According to the means employed in altering the dimensions, the curvatures of plants may be divided into GROWTH-CURVATURES, VARIATION MOVEMENTS DEPENDING ON TURGESCENCE, and HYGROSCOPIC MOVEMENTS. Since growth and osmotic pressure are vital phenomena, *i.e.* are essentially influenced by the living protoplasm, they will be treated below along with the locomotory movements which are dependent on the living substance of the plant. The hygroscopic movements, on the other hand, are not vital phenomena; they occur in dying or dead organs and are brought about exclusively by external factors. The protoplasm only plays a part in these movements in that it has led to such a construction of the organs that changes in the amount of water present produce curvatures and not a simple change in length.

A. Hygroscopic Movements

Two quite distinct types of movement are included in the hygroscopic movements. In the first, which are termed IMBIBITION MECHANISMS ([95]), the cell walls increase in size on swelling or contract on shrinking.

The swelling or shrinking depends on the fact that the water of imbibition is not contained in cavities like those in a porous body (such as a sponge or a piece of plaster of Paris) that contain the capillary water, but in being absorbed has to force apart the minute particles of the cell wall. Conversely these particles approach one another again when the imbibition water evaporates. When on different sides of an organ there are unequally well-developed layers, or layers that swell with unequal rapidity, or when opposite layers differ in the direction of their greatest extension on swelling, curvatures must take place every time the organ is moistened or dries. Though we are here dealing with purely physical phenomena, they may possess great importance for the plant.

The rupture of ripe seed-vessels, as well as their dehiscence by the opening of special apertures, is a consequence of the unequal contraction of the cell walls due to desiccation. At the same time, by the sudden relaxation of the tension, the seeds are often shot out to a great distance (*Euphorbia*, *Geranium*, etc.). This dehiscence on drying is termed XEROCHASY, and is contrasted with the opening of the fruits and dispersal of the seeds in some desert plants when they are moistened (HYGROCHASY). The best example of this is the fruit of *Mesembryanthemum linguiforme*. The behaviour of the "Rose of Jericho" (*Anastatica hierochuntica*) is similar. The whole plant when fruiting dries up, and owing to the unequal shortening of the upper and under sides of the branches becomes contracted into a spherical mass. On the addition of water, the plant resumes its original form, its fruits open and shed the seeds which are thus under favourable conditions for germination. With *Anastatica* some other plants (*e.g. Odontospermum*) may be mentioned, to some of which the name Rose of Jericho is also applied. In certain fruits not only curvatures but torsions are produced as the result of changes in the

amount of water they contain, *e.g. Erodium gruinum* (Fig. 275), *Stipa pennata*, *Avena sterilis*; by means of these, in conjunction with their stiff barb-like hairs, the seeds bury themselves in the earth.

The opening or closing of the moss sporogonium is, in like manner, due to the hygroscopic movements of the teeth of the peristome surrounding the mouth of the capsule. In the case of the Equisetaceae the outer walls of the spores themselves take the form of four arms, which, like elaters, are capable of active movements.

In order to call forth imbibition movements the actual presence of liquid water is not necessary, for the cell walls have the power of absorbing moisture from the air. They are hygroscopic, and are used to estimate the humidity of the air in hygrometers and weather-glasses.

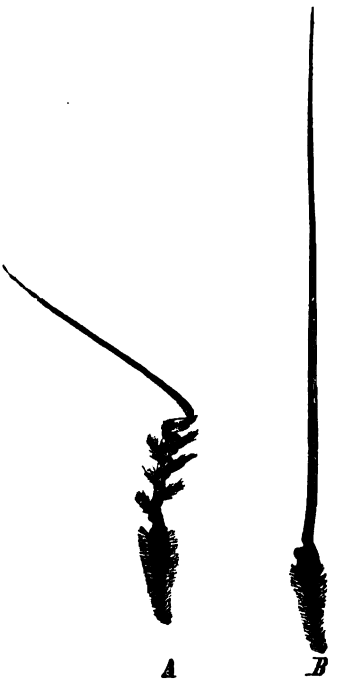


FIG. 275.—Partial fruit of *Erodium gruinum*. *A*, in the dry condition, coiled; *B*, moist and elongated. (After NOLL.)

The mechanisms which depend on the cohesive power of water are distinguished from those depending on imbibition. The COHESION MECHANISMS were previously confounded with the latter, from which they differ in that, even during the movement, the cell walls remain saturated with water. It is the lumen of the cell which diminishes in size when the loss of water, on which the movement depends, occurs. A good example is afforded by the movements of the sporangium of the Polypodiaceae on drying. The sporangia are stalked, biconvex bodies containing the spores within a wall composed of one layer of cells. While the rest of the wall is composed of thin walled cells, one row of peculiarly thickened cells forms a vertically placed semicircle (Fig. 276 *R*). The cells of this ANNULUS have their outer walls thin, the lateral walls increasingly thickened from the outside inwards, and the inner walls thick. On exposure to dry air the cells of the annulus gradually lose the contained water. The watery contents do not, however, separate from the cell wall nor does a rupture occur in the liquid, since the adhesion to the wall and the cohesion of the molecules of water is very great, amounting to hundreds of atmospheres ([96]). A deformation of the cell wall, therefore, follows the diminishing water-content; the thin outer wall (Fig. 276, 3) is pulled inwards, thus approximating the thickened lateral walls. There thus comes about an energetic one-sided shortening

of the annulus which leads to the opening of the sporangium and the shedding of the spores. With further loss of water the contained water ultimately tears apart from the wall, an air-filled space appears, and the cells of the annulus resume their original form. Since this occurs suddenly, the majority of the spores are forcibly thrown out, as the sporangium again closes. The sporangia of other Vascular Cryptogams and the walls of pollen-sacs afford in their opening other examples of cohesion-mechanisms.

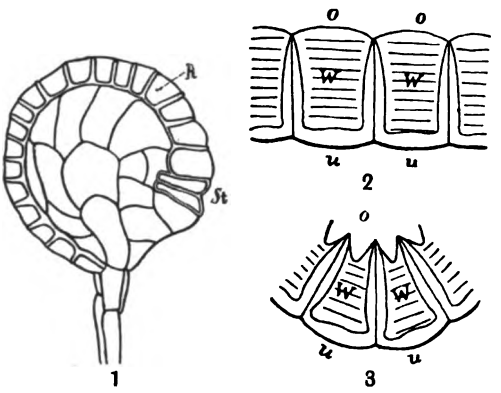


FIG. 276.—1, Sporangium of *Polypodium falcatum*. (After CAMPBELL.) 2, Cells of annulus in original position. 3, After partial evaporation of the water filling them (*w*); the upper cell wall (*o*) is curved in, while the lower (*u*) retains its original length. (2, 3 after NOLL.)

Many hygroscopic curvatures also depend on the co-operation of movements depending on imbibition and on cohesion.

B. Movements of Curvature in the Living Plant

As in the case of plants which exhibit active locomotion, the phenomena of movement in attached plants may occur when all the general conditions of vital phenomena are present, but sometimes only when a particular factor (stimulus) is acting. The latter determines either the amount of the curvature only or its direction also. Movements which take place without such specific external stimuli are termed AUTONOMIC, while the others are termed INDUCED or PARATONIC movements.

1. Autonomic Movements of Curvature

As stated above, a sufficient intensity of the external factors with which life is associated (p. 218) is sufficient to call forth these movements. Beyond a certain minimum and maximum a condition of rigor in which the plant is motionless occurs. Thus, states of rigor due to heat, cold, darkness, dryness, etc., are known.

Thus also the growth of the shoot or root in a straight line (with the characteristic grand period of growth, dependent, as has been shown, wholly on internal causes) is an autonomic movement. A number of growth curvatures or nutations are associated with this

growth, and it might almost be said that there is hardly such a thing as growth in a straight line. The tips of the organs describe extraordinarily irregular curves in space; they exhibit "circumnutations," as was discovered by DARWIN. While these curvatures are usually so slight as not to be perceptible without the aid of special methods, cases exist in which organs exhibit very conspicuous, striking, and regular autonomic growth curvatures.

The unfolding of most leaf and flower buds, for example, is a nutation movement which is induced by the more vigorous growth of the upper side of the young leaves (epinasty). The same unequal growth, in this case of the under side, manifests itself most noticeably in the unrolled leaves of Ferns and many Cycadeae (hyponasty). The stems of many seedlings are, on their emergence from the seeds, strongly curved, and this aids them in breaking through the soil. By the nutation of the shoots of the Wild Vine (*Parthenocissus quinquefolia*) a curvature is produced which continuously advances with the increased growth.

When the unequal growth is not confined to one side, but occurs alternately on different sides of an organ, the nutations which result seem even more remarkable. Such movements are particularly apparent in the flower-stalk of an Onion, which, although finally erect, in a half-grown state often curves over so that its tip touches the ground. This extreme curvature is not, however, of long duration, and the flower-stalk soon becomes erect again and bends in another direction.

If the line of greatest growth advances in a definite direction around the stem, the apex of the latter will exhibit similar rotatory movements (REVOLVING NUTATION). This form of nutation is characteristic of the tendrils and shoots of climbing plants, and facilitates their coming in contact with a support.

Besides these nutations which result from growth, autonomic variation movements are also met with, though less commonly. They are almost confined to foliage leaves, and indeed to those which have pulvini at the base of the petiole and of its further ramifications. Pulvini occur especially in Leguminosae and Oxalideae, also in *Marsilia*, and are characterised by a structure which fits with their particular function.

In the ordinary parenchymatous cell the cell wall, owing to its growth in thickness, ceases to be stretched; on plasmolysis it therefore does not in full-grown cells contract in the same degree as it does in growing cells (cf. Fig. 237). Conversely on an increase of the internal pressure the wall only becomes slightly stretched. In some cases, however, and the pulvinus is an example, the cell walls even in their fully-grown state are considerably distended by the osmotic pressure. This is shown not only by their behaviour on plasmolysis, but also by the persistence of marked tissue-tensions.

A pulvinus of one of the Leguminosae, such as the Kidney Bean, has the vascular bundle and the sclerenchyma, which are peripherally arranged in the leaf-stalk, united to form a central and easily-bent strand; this is surrounded by a thick zone of parenchyma (Fig. 277, 3). If from a pulvinus isolated by two transverse sections the middle sheet of tissue is cut out (Fig. 277, 1), the bulging of the cortical parenchyma both above and below shows the considerable tension. On

splitting the portion of the pulvinus longitudinally as in Fig. 277, 2, the tendency towards expansion of the parenchyma, especially of its middle layers, is very clearly shown.

It will now be readily seen that an increase in turgescence on all sides will increase the tension between the vascular bundle and the parenchyma and thus increase the rigidity of the pulvinus. On the other hand, an increase of turgescence on one side or a diminution on the other side, or the occurrence of both these changes together, will cause a lengthening of the one side and a shortening of the other side which naturally curves the pulvinus. The vascular bundle is passively bent, and undergoes no alteration in length. The passive movement of the part of the leaf attached to the pulvinus is due to the curvature of the pulvinus.

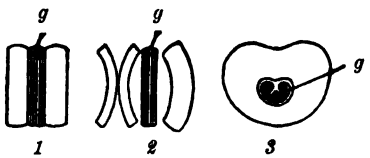


FIG. 277.—Pulvinus of *Phaseolus* (after SACHS). *1*, Layer cut longitudinally from the middle of the pulvinus; *2*, the same cut up; *3*, transverse section. *g*, Vascular bundle.

Autonomic variation movements are probably present in all leaves provided with pulvini, but only attain a striking degree in a few plants.

Thus the small lateral leaflets of *Desmodium gyrans* move uniformly or move interruptedly in elongated ellipses. At higher temperatures (30-35° C.) the movement is very rapid, the course being completed in half a minute. The movement of the leaflets of *Oxalis hedysaroides* is still more rapid, the tip moving through 0·5-1·5 cm. in one or a few seconds. While the autonomic movements of these two plants do not appear to be affected by light, those of *Trifolium pratense* are completely suppressed in light. In the dark, however, the terminal leaflet exhibits oscillatory movements with an amplitude that may exceed 120°; these are regularly repeated in periods of two to four hours.

2. Paratonic Movements (Stimulus Movements) (97)

In the induced or paratonic movements an external factor always acts as a stimulus and starts the movement. By means of these movements attached organisms bring their organs into the positions in which their functions can be best carried out. If the organs of a seedling continued to grow on in the directions which have been accidentally brought about on sowing the seed, the root would often grow into the air and the shoot into the soil.

Light, heat, gravity, and chemical or mechanical influences of the most various kind enable the plant to orientate itself in its environment. The different organs of a plant often show quite different reactions to the same external stimulus. Thus the stem and root, while both tending to place themselves in the direction of the rays of light, grow towards or away from its source respectively; the leaves, on the

other hand, place their flat surfaces at right angles to the incident rays. The mode of reaction is not determined once and for all, but can be profoundly modified. The tone of the plant is thus altered, the change being brought about by either internal or external factors.

The condition of receptiveness to stimuli in the plant is common to all irritable movements and indeed all irritable phenomena. It largely depends on external factors. The same factors that give rise to the stimulus may also intensify or weaken the receptiveness. Other substances, such as the narcotics so well known in animal physiology, may blunt the receptiveness. The stimulus must give rise to definite changes in the plant; the protoplasm must react to these changes in such a way that the characteristic externally visible reaction ultimately takes place. Between this result and the reception of the stimulus there doubtless intervene many and complicated processes which are at present but little understood. The places where the stimulus is received and perceived are termed sense organs or, better, organs of perception. There is particular reason to distinguish organs of perception, when it can be shown that the place where a stimulus is received is separated in space from the part where the movement is effected. In such a case a conduction of the stimulus must take place.

The power of perception or of sensation in the plant can be spoken of without implying any subjective perception, will, or thought, as in the complicated human psychology. This is unfortunately sometimes done by modern sensational writers. The existence of a "soul" in the plant can neither be denied nor asserted (98). No conclusion in this respect can be drawn from the fact that certain features of stimulus movements take place in a similar way to our perceptions. These regularities, which will be later referred to as showing a relation between the intensity of the stimulus and the excitation (p. 347) are, however, of the greatest interest.

Those movements which bring about a particular position with regard to the direction of action of the stimulus may be grouped together as MOVEMENTS OF ORIENTATION or TROPISMS. The other movements of curvature, leading to the assumptions of definite positions with respect to the plant and not to the direction of the stimulus, are termed NASTIC movements.

(a) Tropisms

In the movements of orientation we have to distinguish orthotropous (parallelotropous) and plagiotropous organs. The former place themselves in the direction of the stimulus and approach the source of the stimulus (positive reaction) or move away from it (negative reaction). Plagiotropous organs place themselves at right angles to the direction of the stimulus or obliquely to its direction. The mode of reaction of any particular organ may be changed by external or internal factors. The movements of orientation are distinguished as phototropic, geotropic, etc., according to the stimulus bringing them about.

The tropisms of attached plants correspond to the tactic movements of motile

plants. As in the case of the latter, their significance lies in the attainment of favourable conditions of life. The effective stimulus, the positive and negative modes of reaction, and the alternation from one to the other are completely analogous to the phenomena already described in relation to tactic movements.

1. GEOTROPISM (99)

It is a matter of experience that the trunks in a Fir wood are all vertical, and therefore parallel to one another; the branches and leaves of those trees, on the other hand, take other positions. If, instead of a tree, we consider a seedling, for example of the Maize, we find that, at any rate to begin with, the organs stand in the vertical line. At the same time we here observe more readily than in the case of a tree the totally different behaviour of the roots and the stem, the former growing vertically downwards and the latter upwards. If we bring the seedling from its natural position and lay it horizontally we find that a curvature takes place in both organs; the root curves downwards, and the shoot of the seedling upwards. Since these curvatures are not effected at the region where the root passes into the shoot, but in the neighbourhood of the apices of the two organs, a region of variable length remains horizontal, and only the two ends of the plant are brought by the curvature back into their natural directions, and continue to grow in them. That this vertical growth of the main root and main stem is due to gravity is apparent from direct observation, which shows that these organs are similarly oriented all over the globe, and lie in the direction of radii of the earth. The only force acting everywhere in the direction of the earth's radius that we know of is gravity. Not, however, as a result of this line of thought, but from the experiments of KNIGHT (1806), was this knowledge introduced into our science. KNIGHT'S experiments rest on the following consideration. It is evident that gravity can only cause the root to grow downwards, and the stem to grow upwards, if the seed is at rest and remains in the same relative position to the attractive force of the earth. From this KNIGHT conjectured "that this influence could be removed by the constant and rapid change of position of the germinating seed, and that we should further be able to exert an opposite effect by means of centrifugal force."

He therefore fastened a number of germinating seeds in all possible positions at the periphery of a wheel, so that the root on emerging would grow outwards, inwards, or to the side, and he caused the wheel to rotate round a horizontal axis. Since this rotation was very rapid, not only was the one-sided action of gravity excluded, but at the same time a considerable centrifugal force was produced, which in its turn influenced the seedlings. The result of the experiment was that all the roots grew radially away from, and all the shoots radially towards the centre of the wheel. Thus the

centrifugal force determined the orientation of the seedlings as gravity does normally.

In another experiment KNIGHT allowed gravity and centrifugal force to act simultaneously but in different directions on the seedlings. The plants were fastened on a wheel which rotated round a vertical axis. When the distance of the plants from the centre and the rapidity of rotation were so adjusted that the mechanical effects of the centrifugal force and of gravity were equal, the roots grew outwards and downwards at an angle of 45° and the stem inwards and upwards at the same angle. As the rapidity of rotation increased, the axis of the seedlings took a position approximating more to the horizontal. It results from these experiments that the plant does not discriminate between gravity and centrifugal force, and that the one can be replaced by the other. Both these forces have this in common, that they impart to bodies an acceleration of mass.

An essential addition to the fundamental researches of KNIGHT was given much later (1874) by the experiments of SACHS. In these the plants were rotated round a horizontal axis as in KNIGHT'S first experiment, but the rotation was slow, taking ten to twenty minutes to effect one complete rotation. This is so slow that no appreciable centrifugal force is developed. Since, however, by the continual rotation any one-sided influence of gravity is eliminated, the roots and shoots grow indifferently in the directions which they had at the beginning of the experiment. In this experiment SACHS employed a piece of apparatus termed the KLINOSTAT.

The property of plants to take a definite position under the influence of terrestrial gravity is termed GEOTROPISM. It has been seen that there are not only orthotropous organs which place themselves in the direction of gravity, and grow positively geotropically (downwards) or negatively geotropically (upwards), but also plagiotropous organs which take up a horizontal or oblique position. The positions assumed by the lateral organs are also—though as a rule not exclusively—determined by gravity.

All vertically upward-growing organs, whether stems, leaves (Liliiflorae), flower-stalks, parts of flowers, or roots (such as the respiratory roots of *Avicennia* (Fig. 188), Palms, etc.), are negatively geotropic. When such negatively geotropic organs are forced out of their upright position, they assume it again if still capable of growth. In negatively geotropic organs, growth is accelerated on the side towards the earth; on the upper side it is retarded. In consequence of the unequal growth thus induced, the erection of the free-growing extremity is effected. The actual course of the directive movement of geotropism, as will be seen from the adjoining figure (Fig. 278), does not consist merely of a simple, continuous curvature. The numbers 1-16 show, diagrammatically, different stages in the geotropic erection of a seedling growing in semi-darkness and placed in a

horizontal position (No. 1). The growth in the stem of the seedling is strongest just below the cotyledons, and gradually decreases towards the base. The curvature begins accordingly close to the cotyledons, and proceeds gradually down the stem until it reaches the lower, no longer elongating, portions. Owing to the downward movement of the curvature, and partly also to the after effect of the original stimulus, the apical extremity becomes bent out of the perpendicular (No. 7), and in this way a curvature in the opposite direction takes place. For two reasons this excessive curvature must again diminish (13-16); the stem is now exposed to another geotropic stimulus in the opposite direction to the first, and this is combined with a tendency to straighten, which is termed AUTOTROPISM ([100]).

Every geotropic curvature flattens out or disappears when the plant, before full growth has taken place, is caused to revolve on the klinostat. Since in this case the geotropic stimulus is wanting, some other cause must underlie the straightening. It appears, in fact, that every change in the condition of curvature of an organ, whether resulting from geotropism or from some other cause, acts as a stimulus. The plant works towards a restoration of the original condition, and this tendency is termed autotropism. An organ which was originally straight thus tends by autotropism to return to this condition when curved in any way, either by growth or by mechanical bending. Similarly a curved organ tends to regain its original form when this has been for any cause lost.

In some cases negatively geotropic curvatures may take place in full-grown ([101]) shoots, *i.e.* in such as no longer exhibit growth in length when not geotropically stimulated. Thus in woody stems and branches the growth in length of the cambium of the lower side may bring the organ into the erect position as a result of geotropism. The greater the resistance of the parts which have to be passively bent the more slow and incomplete will this response be. The so-called nodes of grasses, which in reality are leaf-cushions,

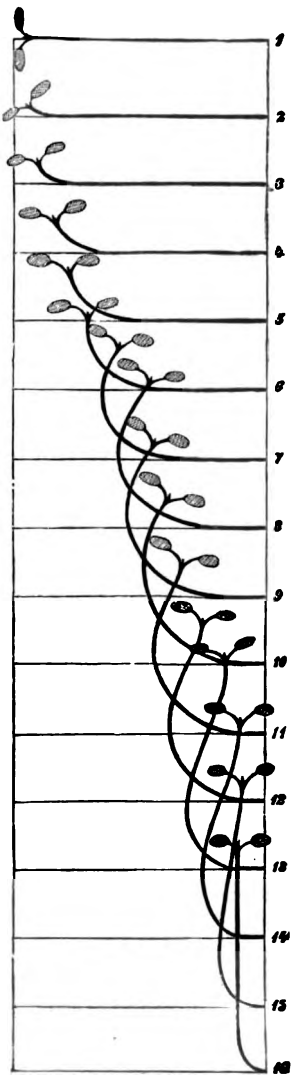


FIG. 278.—Different stages in the process of geotropic movement. The figures *1-16* indicate successive stages in the geotropic curvature of a seedling grown in semi-darkness: at *1*, placed horizontally; at *16*, vertical. For description of intermediate stages see text. (After NOLL. Diagrammatic.)

can also be stimulated by geotropism to further growth. If the stimulus acts on all sides, as when the node is horizontally placed and rotated on the klinostat, all the parenchymatous cells exhibit a uniform elongation. If the node is simply placed horizontally the growth is limited to the lower side while the upper side is passively compressed (Fig. 279). By means of such curvatures in one or several nodes grass haulms laid by the wind and rain are again brought into the erect position.

Positive geotropism is exhibited in tap-roots, in many aerial roots, and in the leaf-sheaths of the cotyledons of some Liliaceae and in the rhizome of *Yucca*. All these organs, when placed in any other position, assume a straight downward direction and afterwards maintain it. Positively geotropic, like negatively geotropic, movements are possible only through growth. The power of a downward curving root-tip to penetrate mercury (specifically much the heavier), and to overcome the resistant pressure, much greater than its own weight, proves conclusively that positive geotropism is a manifestation of an active process. Positive geotropic curvature is due to the fact that THE GROWTH OF AN ORGAN IN LENGTH IS PROMOTED ON THE UPPER SIDE, AND RETARDED ON THE SIDE TURNED TOWARDS THE EARTH. Fig. 280 represents the course of the geotropic curvature in a root.

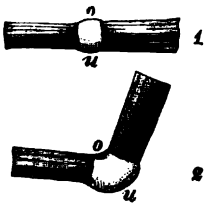


FIG. 279.—Geotropic erection of a grass-haulm by the curvature of a node. *1*, Placed horizontally, both sides (*u*, *o*) of the node being of equal length; *2*, the under side (*u*) lengthened, the upper side (*o*) somewhat shortened; as a result of the curvature the grass-haulm has been raised through an angle of 75°. (After NOLL.)

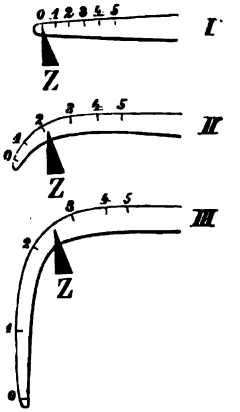


FIG. 280.—Geotropic curvature of the roots of a seedling of *Vicia Faba*. *I*, Placed horizontally; *II*, after seven hours; *III*, after twenty-three hours; *Z*, a fixed index. (After SACHS.)

Most lateral branches and roots of the first order are plagiogeotropic, while branches and roots of a higher order stand out from their parent organ in all directions. THESE ORGANS ARE ONLY IN A POSITION OF EQUILIBRIUM WHEN THEIR LONGITUDINAL AXES FORM A DEFINITE ANGLE WITH THE LINE OF THE ACTION OF GRAVITY. If forced from their normal inclination they return to it by curving. A special instance of plagiogeotropism is exhibited by strictly horizontal organs, such as rhizomes and stolons, which, once they have attained their proper depth, show a strictly TRANSVERSE GEOTROPISM (diageotropism). Should the proper depth not be

attained, the plant tends towards it by upwardly or downwardly directed movements, and then takes on the horizontal growth. The oblique position naturally assumed by many organs is in part the result of other influences.

A special form of geotropic orientation is manifested by dorsiventral organs, *e.g.* foliage leaves, zygomorphic flowers (p. 72). All such dorsiventral organs, just as radial organs that are diageotropic, form a definite angle with the direction of gravity, but are only in equilibrium when the dorsal side is uppermost. In the orientation of dorsiventral organs, not merely simple curvatures but torsions are concerned.

The rotation of the ovaries of many Orchidaceae, of the flowers of the Lobeliaceae, of the leaf-stalks on all hanging or oblique branches, of the reversed leaves (with the palisade parenchyma on the under side) of the Alstroemeriae, and of *Allium ursinum*, all afford familiar examples of torsion regularly occurring in the process of orientation.

The foliage leaves which possess pulvini must again be specially mentioned among dorsiventral organs since they can change their position by geotropic variation movements in the fully-grown state.

Twining Plants ([102]), which are found in the most various families of plants, have shoots which require to grow erect but are unable to support their own weight. The erect stems of other plants, which often secure their own rigidity only by great expenditure of assimilated material (in xylem and sclerenchyma), are made use of by stem-climbers as supports on which to spread out their assimilatory organs in the free air and light. The utilisation of a support produced by the assimilatory activity of other plants is a peculiarity they possess in common with other climbers, such as tendril- and root-climbers. Unlike them, however, the stem-climbers accomplish their purpose, not by the help of lateral clinging organs, but by the capacity of their main stems to twine about a support. The first internodes of young stem-climbers, as developed from the subterranean organs which contain the reserve food material, as a rule stand erect. With further growth the free end curves energetically to one side and assumes a more or less oblique or horizontal position. At the same time the inclined apex begins to revolve in circles like the hand of a watch. This movement continues from the time of its inception as long as the growth of the shoot lasts, and as a rule takes place in a definite direction. In the majority of twining plants the circling movement as seen from above is in the direction opposite to that of the hands of a watch (towards the left as we commonly express it). The Hop and the Honeysuckle twine to the right, in the direction of the hands of a watch. In *Bowiea volubilis* and *Loasa lateritia* a rotation alternately to the right and left has been observed. The plants that circle to the left are also left-handed climbers, *i.e.* the spiral which their stems form (Fig. 281 *I*) mounts from the left to the right and, as seen from above, against the direction of the hands of a watch. Similarly the plants that circle to the right are right-handed climbers. There is thus a close relation between the revolving movement and the twining.

The revolving movement is regarded by some authors as purely autonomic (p. 336); on the other hand, it is held that gravity has a determining influence upon it. This disputable question is still unsettled.

The commencement of the revolving movement does not by itself determine a twining movement. This only begins when the shoot meets a more or less vertical and not too thick support. This is enclosed in loose and at first very horizontal spirals which gradually become more erect and steeper. The straightening results from negative geotropism and leads under otherwise favourable conditions when the support is subsequently removed to a complete obliteration of the spiral coils, the straightened stem appearing twisted. If the support is not removed it leads to tightening of the spiral and increased pressure on the support. The twining movement thus comes about by the revolving movement together with negative geotropism. The support plays a part in that it prevents the otherwise inevitable straightening. It must stand more or less vertically, because otherwise it would not be continually grasped by the overhanging tip of the shoot.

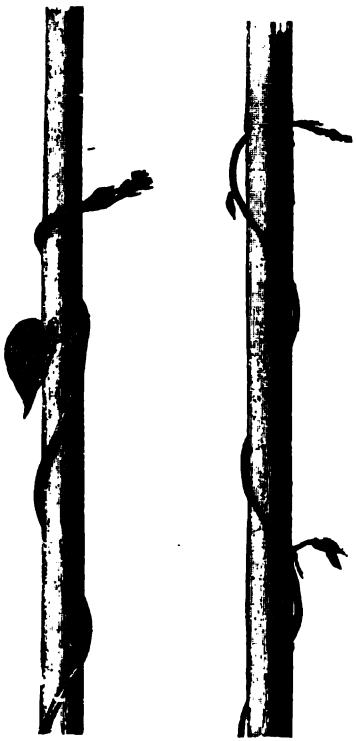


FIG. 281.—*I*, Sinistrorse shoot of *Pharbitis*. *II*, Dextrorse shoot of *Myrsiphyllum asparagoides*. (After NOLL.)

The twining is further assisted by the shoots of the twining plant having to begin with elongated internodes while the leaves remain small. In this respect these shoots resemble those of etiolated plants; the delayed unfolding of the leaves allows of the regular circling of the tip which might otherwise be interfered with by the leaves encountering the support. The firm hold on the support is frequently increased by the roughness of the surface of the stem owing to hairs, prickles, ridges, etc. Torsions also, the causes of which cannot be entered into here, have a similar effect.

Although STARK has recently shown that twining plants are not insensitive to contact with the support (cf. p. 354), it still holds good that the result of this contact does not determine the twining movement.

Alteration of the Geotropic Position of Rest.—The position assumed by an organ as a result of a definite geotropic stimulation

is not determined once and for all, but is liable to change owing to internal and external influences. There is thus a "change of tone" as regards geotropic stimulation. A certain "tone" is thus regarded as the normal one, and the resulting reactions are expressed in the distinction of orthotropous and plagiotropous, and positively and negatively geotropic organs respectively.

Among the external factors which influence the geotropic tone, light, temperature, oxygen, and gravity itself may be mentioned, and as an internal factor the developmental phase of the organ.

The alteration of geotropic reaction by the illumination has an important influence on the depth at which rhizomes occur. When the tip of a rhizome of *Adoxa* growing on a slope becomes exposed to the light, its transverse geotropism

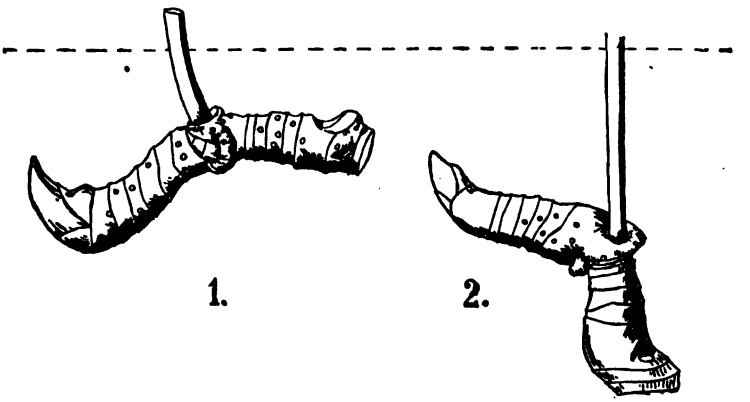


FIG. 282.—Rhizome of *Polygonatum*. The dotted line marks the surface of the soil. The aerial shoots are cut off. Rhizome 1 was planted too high; its continuation is downwards, only the terminal bud which will form a flowering shoot being directed upwards. Rhizome 2 was planted erect and too deep; its continuation is obliquely upwards. (After RAUNKIAER.)

becomes altered to positive geotropism, and this leads to the rhizome again entering the soil. Frequently the influence of light on the parts of the plant above ground suffices to direct the subterranean rhizome. If the rhizome of *Polygonatum* is planted too high in the soil, although covered by earth and in the dark, the new growth turns obliquely downwards; if planted too deeply it turns upwards (Fig. 282). At the correct depth the rhizome is transversely geotropic. Light also acts strongly on the geotropism of lateral roots; when illuminated the lateral roots of the first order approach the orthotropous position of rest much more closely than they do in the dark.

An effect of temperature may be observed on the stems of some spring plants; these often lie on the ground at temperatures in the neighbourhood of 0° C. and only become orthotropous at higher temperatures. With lack of oxygen many roots and rhizomes become negatively geotropic, and thus reach regions where more oxygen is available.

Changes of tone due to internal causes are seen, for instance, in rhizomes, which

at a certain stage of development change from the diageotropic position and become orthotropous, or in inflorescences which become positively geotropic after fertilisation. In this way the fruits of *Trifolium subterraneum* and of *Arachis hypogaea* become buried in the soil. In twining stems also a change of tone has been noted; while young they do not twine.

Geotropism as a Phenomenon of Irritability.—The discoverer of geotropism, KNIGHT, attempted to explain the geotropic movements on purely mechanical lines; this did not seem difficult, especially for positively geotropic organs. He regarded them as simply following the attractive force of gravity till a condition of rest is attained. Later HOFMEISTER advanced similar views. The correct assumption that we are concerned with complicated stimulus mechanisms in which terrestrial gravity only plays the part of the liberating factor depends on the work especially of DUTROCHET, FRANK, and SACHS. Even the single fact that the root can carry out its geotropic curvature against the resistance of mercury is sufficient to call in question every purely mechanical explanation.

Only in recent times has the attempt been made to determine what is the primary effect of gravity in the plant ([108]). There is no doubt that we are concerned with an effect of pressure; the fact that gravity can be replaced by centrifugal force is in favour of this. This effect of pressure only comes into action in the case of orthotropous organs in proportion as it acts at right angles to the longitudinal axis, and thus in relation to the vertical component when the organ is placed obliquely. Lastly, it is clear that the pressure must act within the cells, and is in no way replaceable by external influences.

It is not known whether this pressure is determined by the entire cell-contents and acts on the protoplasm as a whole, or whether special organs are concerned in its production and reception. Various hypotheses on this question have been advanced. F. NOLL first elaborated the idea that there must be some bodies in the cells of greater specific gravity than the surrounding protoplasm, and capable, under the influence of gravity, of exerting a one-sided pressure on the protoplasm; on this taking place the protoplasm directs the processes of growth in accordance with the direction of the force of gravity. NĚMEC and HABERLANDT then suggested that these specifically heavier bodies (statoliths) might be found in certain starch grains which show relatively rapid movements of falling in the cells. They found such starch grains in the endodermis of the stem and in the cells of the root-cap. They assume that the stimulus of gravity can only directly affect portions of the plant provided with such starch grains, but that it may be conducted from these points to others. As a matter of fact the attempt had previously been made to show that only the tip of the root can receive the gravitational stimulus. Even at the present time this question is not decided, and not a few investigators assume that all cells—though in various degrees—are geotropically sensitive. Thus fungi, in which statoliths are not found, are geotropic. The hypothesis of NĚMEC and HABERLANDT, though there is much in its favour, is not fully established. HABERLANDT himself states that in certain

cases (moss-rhizoids) geo-perception is still possible after the disappearance of starch. If, however, the investigations of ZOLLIKOFER are confirmed, according to which, after disappearance of the starch, the power of geotropic reaction is lost, while growth and phototropic reactions continue, the statolith-hypothesis would have received the long-sought support.

As a rule we can only infer the geotropic irritability of an organ from the curvatures that take place, but in some cases it can be done independently of this reaction. Thus, for example, in some grass seedlings (Paniceae) that have a well-developed internode beneath the sheathing leaf, the latter becomes full grown and no longer capable of curvature; it is, however, still geotropically sensitive, since on the sheath being exposed to the one-sided action of gravity the internode below, which is not itself sensitive to the stimulus, becomes curved. The geotropic stimulus must have been conducted from the sheathing leaf to the internode. In other grass seedlings (Poaeoideae) it has been observed that the tip of the sheath is much more sensitive to the geotropic stimulus than the zone of maximal growth, and a similar diminution of the sensibility on passing backwards from the tip holds for roots. It is possible with special apparatus to stimulate geotropically in opposite directions the apex and growing zone of such objects by centrifugal force, and to show that the curvature of the growing zone is then determined by the stimulated tip. There is thus a conduction of the stimulus in the basal direction which overcomes the direct stimulation of the growing zone. In such cases a clear separation of three processes is evident, the reception of the stimulus (perception), the conduction of the stimulus and the reaction. An organ may be perceptive without being able to react or conversely. We are justified in assuming that these three parts of the process must be distinguished in cases where they are not so evident.

It can be inferred from these experiments that the degree of geotropic curvature and the rapidity with which it is produced in no way measures the amount of the stimulus, since they are largely dependent on the capacity for growth. The degree of geotropic stimulation depends both on the specific receptivity of the stimulated organ and on the amount of stimulus which it has received. For any given organ it is directly proportional to the amount of stimulus. By this is understood the product of the intensity of the stimulus and the duration of its action. Thus, it is the same so far as result is concerned, whether a high centrifugal force for a short time or a less force for a correspondingly longer time be employed.

This law ([104]) holds good only within certain limits. It has been shown that an orthotropous organ, when laid horizontally under constant external conditions, begins to curve after a definite time. The period from the commencement of stimulation to the commencement of the reaction is termed the REACTION-TIME. To obtain a geotropic reaction, however, it is not necessary to stimulate an organ

during the whole reaction-time. A much shorter period of stimulation is sufficient to obtain a geotropic curvature as an after effect from the organ which has been replaced in the vertical position. The minimal period of stimulation after which a visible curvature results is termed the PRESENTATION-TIME. The law of amount of stimulus only applies to stimuli which last as long or somewhat longer than the presentation-time; the presentation-time is thus inversely proportional to the intensity of the stimulus. No corresponding increase of geotropic curvature follows larger amounts of stimulus.

Stimuli below the presentation time are not without effect. On repetition they are summed up and result in a curvature when the sum of separate stimuli amounts to the presentation-time, if the intervals between the separate stimuli have not been too great. A lower limit for the duration of separate stimuli has not as yet been determined.

The law of amount of stimulus also applies when the centrifugal force or gravity acts obliquely on an orthotropous part of a plant. The effect of gravity diminishes in proportion to the sine of the angle of incidence; if at 90° it = 1, it will be = 0·5 at 30°. Thus only the pressure at right angles to the long axis is effective.

2. PHOTOTROPISM (HELIOTROPISM) ([105])

A good opportunity for the observation of heliotropic phenomena is afforded by ordinary window-plants. The stems of such plants do not grow erect as in the open, but are inclined towards the window, and the leaves are all turned towards the light. The leaf-stalks and stems are accordingly ORTHOTROPIC and POSITIVELY PHOTOTROPIC. In contrast to these organs the leaf-blades take up a position at right angles to the rays of light in order to receive as much light as possible. They are DIAPHOTOTROPIC, or TRANSVERSELY HELIOTROPIC, in the strictest sense. If among the plants there should be one with aerial roots, *Chlorophytum* for instance, an example of NEGATIVE PHOTOTROPISM will be afforded, as the aerial roots will be found to grow away from the window and turn towards the room. In Fig. 283 the phototropic curvatures which take place in a water culture of a seedling of the White Mustard are represented.

Sensibility to phototropic influences is prevalent throughout the vegetable kingdom. Even organs like many roots, which are never under ordinary circumstances exposed to the light, often exhibit phototropic irritability. Positive phototropism is the rule with aerial vegetative axes. Negative phototropism is much less frequent; it is observed in aerial roots, and sometimes also in climbing roots (*Ficus stipulata*, *Begonia scandens*), in the hypocotyl of germinating Mistletoe, in many, but not all, earth roots (*Sinapis*, *Helianthus*), in tendrils (chiefly in those with attaching discs), and in the stems of some climbers. By means of their negative heliotropic character, the organs for climbing and attach-

ment, and the primary root of the Mistletoe, turn from the light towards, and are pressed firmly against, their darker supports.

For more exact investigation of phototropic movements it is necessary to be able to control more accurately the source and direction of the light. This can be best accomplished by placing the plants in a room or box, lighted from only one side by means of a narrow opening or by an artificial light. It then becomes apparent that the direction of the incident rays of light determines the phototropic position; every alteration in the direction of the rays produces a change in the position of the phototropic organs. The apical ends of many positively heliotropic organs will be found to take up the same direction as that of the rays of light.

The exactness with which this is done is illustrated by an experiment made with *Pilobolus crystallinus* (Fig. 284). The sporangiophores of this fungus are quickly produced on moist horse or cow dung. They are positively phototropic, and turn their black sporangia towards the source of light. When ripe these sporangia are shot away from the plant, and will be found thickly clustered about the centre of the glass over a small aperture through which alone the light has been admitted; a proof that the sporangiophores were all previously pointed exactly in that direction.

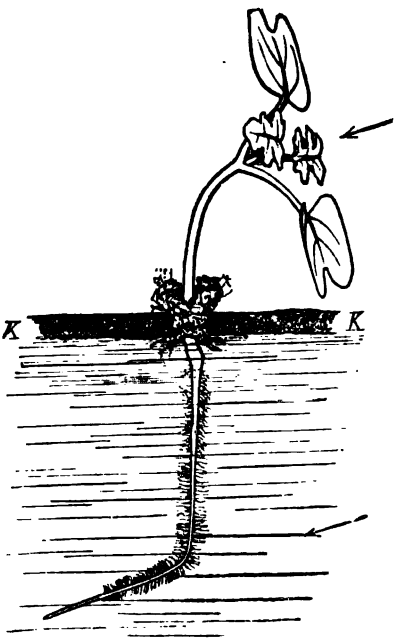


FIG. 283.—A seedling of the White Mustard in a water culture which has first been illuminated from all sides and then from one side only. The stem is turned towards the light, the root away from it, while the leaf blades are expanded at right angles to the incident light. *KK*, Sheet of cork to which the seedling is attached. (After NOLL.)

The positive phototropic curvatures are brought about by THE SIDE TURNED TOWARDS THE LIGHT GROWING MORE SLOWLY, AND THAT AWAY FROM THE LIGHT MORE ACTIVELY, THAN UNDER ILLUMINATION FROM ALL SIDES. The converse distribution of growth is found in negative phototropism. As a rule CURVATURES ONLY TAKE PLACE IN THE REGION WHICH IS STILL IN A GROWING CONDITION, THE SHARPEST CURVATURE BEING AT THE REGION OF MOST ACTIVE GROWTH.

The course of phototropic curvature shows a complete correspondence with geotropic curvature (p. 341). A. ENGLER has recently demonstrated phototropic

curvature even in trees where growth in length had ceased. It was formerly held that the increased growth of the shaded side in positive phototropism was produced by the beginning of etiolation, and that the diminished growth on the illuminated side was due to the retarding effect which light exerts upon growth in length (p. 289). This view has for some time been abandoned for good reasons; it cannot be maintained even in the modified form in which it has been recently stated by BLAAUW [108]. The fact that in many cases the curvature is far removed from the region stimulated by light (p. 351) is especially opposed to this explanation.

It is evident from these considerations that it is not the difference in the intensity of the light which causes the heliotropic curvatures, but the direction in which the most intense rays of light enter the organs. LIGHT ACTS AS A MOTORY STIMULUS WHEN IT PENETRATES AN ORGAN IN ANY OTHER DIRECTION THAN THAT WHICH CORRESPONDS WITH THE POSITION OF HELIOTROPIC EQUILIBRIUM. Only one-sided illumination can thus cause curvature in a plant. If, without altering the direction or the intensity of the illumination, the plant is kept in constant rotation, around a vertical axis, by means of clockwork, the phototropic stimuli acting on the different sides neutralise one another and no curvature takes place. This apparatus is known as a KLINOSTAT.

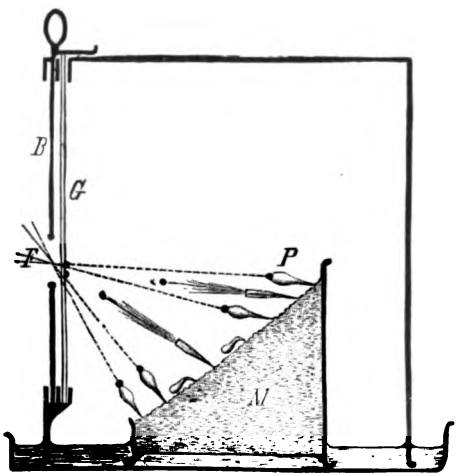


FIG. 284.—*Pilobolus crystallinus* (*P*), abjecting its sporangia towards the light. *G*, Sheet of glass; *B*, opaque case with a circular opening at *F*; *M*, vessel containing horse-dung. (Cf. description in text. After NOLL.)

The phototropic curvatures are most strongly produced, just as in the case of the heliotactic movements of freely moving swarm-spores, by the blue and violet rays, while red and yellow light exerts only a much slighter influence. When a plant receives on one side red light, and on the other side blue light, it turns towards the latter, even when the red light is of greater intensity.

TRANSVERSE PHOTOTROPISM is confined almost solely to leaves and leaf-like assimilatory organs, such as Fern prothallia and the thalli of Liverworts and Algae. In these organs transverse phototropism, in conformity with its great utility for assimilation, predominates over all other motory stimuli. Such organs become placed at right angles to the brightest rays of light to which they are exposed during their development; in this process torsions of the leaves or internodes are combined with the simple curvatures.

In very bright light the transverse position of the leaves may become changed to a position more or less in a line with the direction of the more intense light rays. In assuming a more perpendicular position to avoid the direct rays of the midday sun, the leaf-blades of *Lactuca Scariola* and the North American *Silphium laciniatum* and the leaf-like shoots of some Cacti take the direction of north and south, and so are often referred to as COMPASS PLANTS. The foliage leaf has thus, like the chloroplast of *Mesocarpus*, the power of assuming either a profile or a full-face position, and thus regulating the amount of light received.

A number of foliage leaves possess pulvini (Fig. 132) at the base of the petiole, and also at the bases of secondary and tertiary branchings; variation movements are effected by the aid of these. In this way these leaves are able to change their position throughout life, and at any moment to assume the position which affords them the optimal supply of light. They do not have a fixed light-position determined by the strongest illumination during their development, but they sometimes expose their edges and sometimes their surface to the light.

ALTERATION OF TONE ([107]).—A particular part of a plant does not react always in the same way to one and the same stimulus; the mode of reaction may be altered by age or other influences. In this sense the terms "tone" and "change of tone" are used.

The flower-stalks of *Linaria cymbalaria* are at first positively phototropic. After pollination, however, they become negatively phototropic, and as they elongate they push their fruits into the crevices of the walls and rocks on which the plant grows (p. 281).

Among external factors that alter the tone the amount of illumination itself is particularly important. Small amounts of light falling from one side on *Avena* produce without exception a positive phototropic curvature; larger amounts give a weaker positive soon followed by a negative curvature; still larger amounts give a purely negative reaction. With further increase in the illumination a positive reaction is again obtained, and later a weakened positive if not a negative reaction. How far the intensity of the illumination also influences the results cannot be discussed here.

Phototropism, like geotropism, is a PHENOMENON OF IRRITABILITY ([108]). In it the perception, conduction, and reaction of the stimulus can also be distinguished; there are also presentation-time and reaction-time. Further, the law of amount of stimulus holds, and separate stimuli which are individually ineffective can be added together to produce a reaction.

Localisation of Phototropic Perception.—Often the stimulus of light is received at the same place that the movement is effected. In certain leaves, however, the lamina is able to perceive a phototropic stimulus without being able to carry out the corresponding movement; this takes place only after the stimulus has been conducted to the leaf-stalk. It is true that the leaf-stalk can also react to direct stimulation, but as a rule the dominant impulse proceeds from the lamina. Still more striking relations are met with in the seedlings of certain Grasses; in some Paniceae only the tip of the so-called cotyledon can be phototropically stimulated, and only the hypocotyledonary segment of the stem, separated by some distance

from the tip of the cotyledon, is capable of curvature. In this case there is a well-marked distinction between a perceptive organ and a motile organ; the similarity to corresponding phenomena in geotropism and in the animal kingdom is very striking. There is an essential difference, however, in the method of transmission of the stimulus; "Nerves" are completely wanting in the plant, and the stimulus is conveyed from cell to cell [109].

There is no doubt that the perception of light by the plant is closely connected with photochemical processes. As to how the plant perceives the direction of the light we are, however, ignorant [109a].

3. Chemotropism [110]

In the same way as light and gravity, heat and electricity, when their action is one-sided, may bring about directive movements of the plant. Since, however, these movements play no great part in nature they need not be further considered. Those directive movements which are brought about by the unequal distribution of dissolved or gaseous substances in the neighbourhood of the plant are of much greater importance; these movements are termed chemotropic.

In the case of fungi and of pollen-tubes, chemotropic movements have been demonstrated which bring the organism into a certain concentration of particular substances; this concentration is the optimal one. With the same organism and the same stimulating substance these movements are sometimes positive and sometimes negative; positive when they lead towards a higher concentration of the substance, and negative in the converse case. In the case of pollen-tubes sugar is the chief substance that acts as a stimulus; in fungi, in addition to sugar, peptone, asparagin, compounds of ammonia and phosphates. There are also substances such as free acids which always have a repellent influence even in extremely weak concentration. Chemotropic irritability has also been demonstrated in roots, though it cannot be said that it plays an important rôle in their life.

In the examples of chemotropism given above, the stimulating substances were solid substances in solution. When on the other hand the plant is induced to perform directive movements by the unequal distribution in a space of aqueous vapour or gases, a distinct name has been required, though no distinction of principle can be drawn. Irritable movements caused by differences in moisture are termed HYDROTROPIC, while those brought about by gaseous differences are termed AEROTROPIC. Aerotropism has been proved for pollen tubes, roots, and shoots, and hydrotropism for roots and moulds. Thus roots are positively hydrotropic and seek out the damper spots in the soil by reason of this irritability. The sporangiophores of the Mucorineae are negatively hydrotropic and thus grow out from the substratum. These reactions may be so energetic as to overcome other (*e.g.* geotropic) stimuli.

4. HAPTOTROPISM (THIGMOTROPISM) ([111])

A curvature inwards on one-sided contact is found especially in climbing plants which seek by such grasping movements to encircle the touching body and utilise it as a support. The arrangement thus resembles what was seen in the case of twining plants, but the movements are not in any sense geotropic. In the case of tendril-climbers, the attachment to the support is effected, not by the main axis of the plant, but by lateral organs of various morphological character (cf. p. 182). These may either retain, at the same time, their normal character and functions (as foliage leaves, shoots, or inflorescences), or, as is usually the case, become modified and as typical tendrils serve solely as climbing organs. Contact with a solid body quickly induces an increase in the growth of the opposite side of the organ, and this, without any retardation of growth on the touched side, leads to a sharp curvature of the tendril which coils it about the

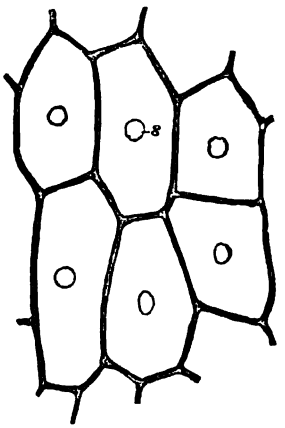


FIG. 285.—Surface views of cells from the sensitive side of the tendril of *Cucurbita Pepo*, showing tactile pits, *s*. (× 540. After STRASBURGER.)

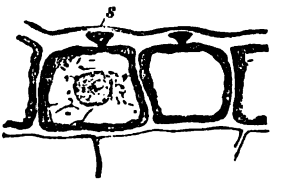


FIG. 286.—Transverse section through similar cells to those in Fig. 68; a small crystal of calcium oxalate (*s*) is present in the tactile pit. (× 450. After STRASBURGER.)

support. The more slender the tendrils and the stronger their growth, the more easily and quickly this process occurs. Owing to the tendency of the curvature to press the tendrils more and more firmly against the support, deep impressions are often made by them upon yielding bodies, soft stems, etc.

According to PFEFFER'S investigations, it is of great importance to the tendrils in the performance of their functions that they are not induced to coil by every touch, but only through CONTACT WITH THE UNEVEN SURFACE OF SOLID BODIES. Rain-drops consequently never act as a contact stimulus; and even the shock of a continued fall of mercury produces no stimulation, while a fibre of cotton-wool weighing 0·00025 mgr. is sufficient to stimulate the tendril. Probably the so-called tactile pits (Figs. 285, 286) favour the reception of such weak stimuli. These are pits in the outer epidermal walls which

widen outwards and are filled with protoplasm. They are found, for instance, in the Cucurbitaceae, but may be wanting from some very irritable tendrils (*e.g.* in *Passiflora*).

The tendrils of some plants (*Cobaea*, *Eccremocarpus*, *Cissus*) are irritable and capable of curving on all sides; others (tendrils of Cucurbitaceae and others with hooked tips) are, according to FITTING, sensitive on all sides but only curve when the under side is touched; if the upper surface is at the same time stimulated, curvature is arrested. Some tendrils, only sensitive on one side, have the tactile pits confined to this. In some cases the tendrils quickly grasp the support (*Passiflora*, *Sicyos*, *Bryonia*); while in other tendrils the supports are very slowly grasped (*Smilax*, *Vitis*).

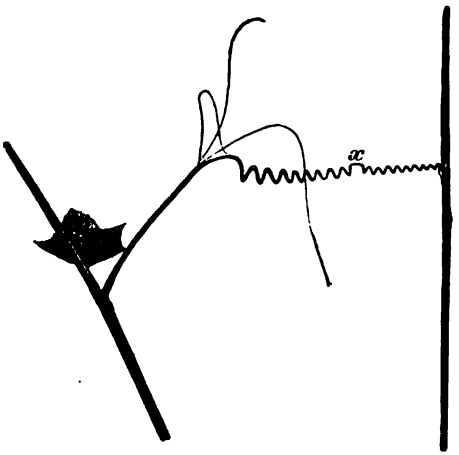


FIG. 287.—Portion of a stem of *Sicyos angulatus*, one of the Cucurbitaceae, with tendril. The branch-tendril has grasped the upright support on the right and the free portion has become spirally wound. *x*, Point of reversal in the coiling of the tendril. (After NOLL.)

In the more typically developed tendrils the curvature does not remain restricted to the portions directly subjected to the action of the contact stimulus. Apart from the fact that, in the act of coiling, new portions of the tendril are being continually brought into contact with the support and so acted upon by the stimulus, the stimulation to curvature is also transferred to the portions of the tendril not in contact with the support. Through the action of the propagated stimulus, not only is the free apex of the tendril twined more quickly around the support, but a tendency to curvature is imparted to the portion of the tendril between the support and the parent shoot. As this intervening part is extended between two fixed points, this tendency causes it to coil spirally, like a corkscrew. With the spiral coiling a torsion is produced, and since, on account of the fixed position of the two end points, it cannot be exerted in one direction only, the spiral, for purely mechanical reasons, coils partly to the left and partly to the right. POINTS OF REVERSAL (*x*) thus occur in the windings which, in equal numbers to the right and to the left, equalise the torsion (Fig. 287). By the spiral coiling of the tendrils the parent-stem is not only drawn closer to the support, but the tendrils themselves acquire greater elasticity and are enabled to withstand the injurious effects of a sudden shock.

Advantageous changes also take place in the anatomical structure of the tendrils after they are fastened to the supports. The young tendrils, during their rapid elongation, which under favourable conditions may amount to 90 per cent of their length, exhibit active nutations, and thus the probability of their finding a support is enhanced. During this time they remain soft and flexible, while the turgor

rigidity of their apices is maintained only by collenchyma. In this condition they are easily ruptured, and have but little sustaining capacity. As soon, however, as a support is grasped, the coiled-up portion of the tendril thickens and hardens, while the other part lignifies and becomes so strengthened by sclerenchymatous formations that the tendril can finally sustain a strain of many pounds. When the tendrils do not find a support they usually dry up and fall off, but in some cases they first coil themselves into a spiral.

Tendril-climbers are not, like twining plants, restricted to nearly vertical supports, although, on account of the manner in which the tendrils coil, they can grasp only slender supports. A few tendril-climbers are even able to attach themselves to smooth walls. Their tendrils are then negatively phototropic, and

FIG. 288.—*Lophospermum scandens* climbing by means of its tendril-like petioles. (After NOLL.)

provided at their apices with small cushion-like outgrowths, which may either develop independently on the young tendrils, or are first called forth by contact irritation. These cushions become fastened to the wall by their sticky excretions and then grow into disc-like suckers, the cells of which come into such close contact with the supporting wall that it is easier to break the lignified tendrils than to separate the holdfasts from the wall. Fig. 210 represents the tendrils of *Parthenocissus tricuspidata*. The suckers occur on its young tendrils in the form of knobs. In other species of Wild Vine the suckers are only produced as the result of contact, and the tendrils of these plants are also able to grasp thin supports.

Sometimes, as in the case of *Lophospermum scandens* (Fig. 288), the leaf-stalks, although bearing normal leaf-blades, are irritable to contact stimuli and function as tendrils. Of leaf-stalks which thus act as tendrils, good examples are afforded by *Tropaeolum*, *Maurandia*, *Solanum jasminoides*, *Nepenthes*, etc. In other cases the midribs of the leaf-blades themselves become prolonged, and assume the function of tendrils (*Gloriosa*, *Littonia*, *Flagellaria*). In many species of *Fumaria* and *Corydalis*, in addition to the leaf-stalks, even the stalks of the

leaflets twine around slender supports, while the parasitic shoots of *Cuscuta* (Fig. 221) are adapted for both twining and climbing. In many tropical plants axillary shoots are transformed into tendril-like climbing hooks. Climbing parts of the thallus occur in some Thallophyta (Florideae).

More recent investigations have shown that haptotropism is more widespread than was previously supposed. Etiolated seedlings are always haptotropic, and this holds frequently for older shoots of green plants, especially of twining and climbing plants. No use appears to attach to this power [112]. The roots of seedlings are only exceptionally irritable to contact.

(b) Nastic Movements [113]

In the tropistic and tactic movements of irritability, the direction of the stimulus stands in direct relation to the direction of the movement; the nastic movements, on the other hand, are either brought about by diffuse stimuli with no definite direction or are not influenced by the direction of the stimulus. The direction of the movement always depends on the reacting organ and not on the environment, the movements are not movements of orientation such as those we have hitherto considered.

Typical nastic movements of variation are shown by stomata; the structural relations of these determines the opening or closing of the pore by changes in the curvature of the guard-cells brought about by variations in their turgescence. It is frequently assumed that the closing on loss of water and the opening on illumination are purely mechanical results. Loss of water will have as its direct result a diminution of the osmotic pressure, and illumination will increase the pressure by increasing the production of assimilates. It cannot, however, be doubted that in addition to purely physical influences true stimulus-movements also take place. Thus light and some other factors also may act as stimuli directing the production of osmotic substances by the protoplasm in particular directions.

In other nastic movements, as in the case of the stomata, light and heat, chemical substances, and sometimes also vibrations, may play the part of stimuli. Often the movement of a particular organ results from several of these stimuli in the same or in different ways.

1. Nyctinastic Movements [114]

Many foliage leaves and floral leaves assume different positions by day and by night. According as the change from the one position to the other is brought about by variations in the intensity of light, in the temperature, or in both factors at once, we distinguish between photonasty, thermonasty, and nyctinasty. The movements are carried out partly as growth-movements, partly as variation-movements.

1. Thermonasty.—Growth-movements due to variations in temperature are found especially in flowers, *e.g.* *Crocus*, Tulip, *Ornithogalum*, *Colchicum*, and *Adonis*. These flowers on a rise of temperature exhibit a sudden and limited acceleration of the growth

of the inner side of their perianth-leaves or petals. The flowers consequently open. On the other hand, they close on a fall in the temperature.

The flowers of the Tulip and Crocus are especially sensitive to changes of temperature. Closed flowers brought from the cold into a warm room open in a short time; with a difference of temperature of from 15°-20° they open in two to five minutes. Sensitive flowers of the Crocus react to a difference of ½° C.; those of the Tulip to 2°-3° C.

2. PHOTONASTY.—In a similar fashion other flowers (*Nymphaea*, Cacti) and also the flower heads of Compositae (Fig. 289) open on illumination and close on darkening. The night-flowering plants such as *Silene noctiflora* and *Victoria regia* behave in an opposite manner.

The significance of these movements must lie in only exposing the sexual organs when insect-visits may be expected; at other times they are protected against injury by rough weather, especially by rain. These plants are adapted to pollination by moths.

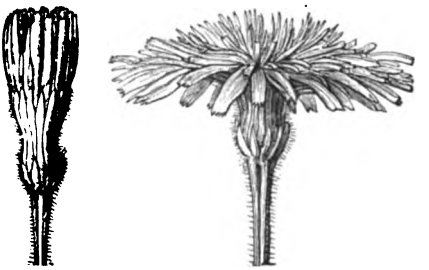


FIG. 289.—Flower-head of *Leontodon hastilis*, closed when kept in darkness, open when illuminated. (From DETMER'S *Physiol. Pract.*)

3. NYCTINASTY.—Many foliage leaves exhibit nyctinastic movements which are usually influenced more by light than by temperature. In some cases (*e.g.* in Chenopodiaceae, Caryophyllaceae, Balsamineae, and some Compositae) these movements are entirely growth-movements as in the floral leaves; in the Leguminosae, Oxalideae, and other plants provided with pulvini, variation-movements are found. The former are naturally of short duration and cease when the leaves are full-grown. The latter, however, continue for a long period. In the movements of variation an increase of turgor probably takes place in darkness in both halves of the pulvinus, but more weakly or slowly on the concave side. The night- or sleep-position is always characterised by a vertical position of the laminae, the leaf-stalk or the pulvinus curving either upwards or downwards; the laminae themselves have thus either their under or upper faces turned outwards. In the day-position the surfaces stand horizontally or at right angles to the incident light (p. 351) (Fig. 290).

That these phenomena are not due to phototropism is shown by the day-position being assumed whether the under or the upper side is more strongly lighted or when the illumination is equal. The same holds for the effect of darkness.

The significance of the vertical position assumed by foliage leaves at night is regarded by STAHL as consisting in the diminution of the formation of dew and the

consequent favouring of transpiration. The fact that the stomata lie on the surface protected in the sleep-position may be noted with regard to the furthering of transpiration.

Excessively high temperature or illumination causes the leaves to depart from the usual day-position and to assume a different one; this is either externally

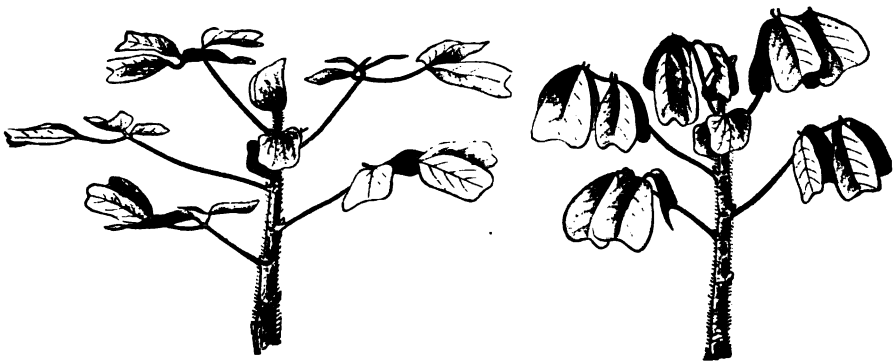


FIG. 290.—*Amicia zygomeris*, showing diurnal and nocturnal position of leaves.

similar to the night-position or is diametrically opposite to this. Thus the leaflets of *Robinia* are bent downwards at night, in diffused daylight they are spread out flat, while in the hot mid-day sunlight they stand vertical. This so-called diurnal sleep is only found in leaves with pulvini and is brought about in a different way to the evening change of position; there is no increase of turgescence but a condition of flaccidity, which is unequal on the two sides of the pulvinus.

PERIODIC MOVEMENTS (115)

When a plant has carried out regular nyctinastic movements for a long period under the influence of the alternation of day and night, the periodic movements continue for some days in constant light or constant darkness. In some plants it is possible to bring about experimentally a shorter or longer period of change than the usual one of twenty-four hours; this new periodicity also shows an after effect.

On the other hand it is established that, in certain flowers (*Calendula*) and leaves (*Phaseolus*), there are also movements with a period of 24 hours, determined not by the rhythm of light and darkness or their after effect. The possibility that these movements are antonomous is excluded. Their cause is unknown but there is much in favour of the view of STOPPEL that variations in the electrical conductivity of the atmosphere are of importance in determining them. It is true that there is no exact basis for this view.

2. CHEMONASTY (116)

Chemonasty bears the same relation to chemotropism as photonasty does to phototropism. From whatever side a chemical stimulus (such as the vapour of ether, chloroform, or ammonia) acts on a sensitive tendril the same side of the latter always becomes concave; this is the side which is especially sensitive to haptotropic stimulation.

These chemonastic curvatures of tendrils are evidently of no use to the plants. The same is the case for the nastic movements of tendrils which take place on wounding and on rise of temperature (traumatonasty, thermonasty). On the other hand, chemonastic movements play an important part in some insectivorous plants.

Very striking chemonastic movements are exhibited by the tentacles of *Drosera* (Fig. 214). On chemical stimulation these curve so that their upper sides become concave and the glandular heads are thus brought towards the centre of the circular leaf. Such substances as albumen, phosphates, etc., which *Drosera* can use as food, serve as stimuli (p. 258); so also can indifferent and even poisonous substances. Often minimal traces of these substances (*e.g.* 0·0004 mgr. of ammonium phosphate) suffice to bring about the irritable movement; when the stimulus is applied to the summit of the tentacle it leads to the curvature at the base of the latter. There is thus in this case as in certain phototropic curvatures, but even more clearly than in these, a separation between the organ of perception which receives the stimulus and the motile organ that effects the movement. The stimulus received by the head of the tentacle must be conducted to the base of the latter.

An insect that has settled on a marginal tentacle will be brought by this curvature to the centre of the lamina. The short-stalked tentacles borne here send a stimulus to all the marginal ones, causing them to curve inwards. The insect is thus surrounded by many glands and covered with their digestive secretion.

The curvature resulting from growth is carried out in the same way as in tendrils. After curvature the tentacle has become considerably longer. When growth ceases, the motility of the tentacles is ended so that they can only close over a limited number of times. Further, the tentacles of *Drosera* in common with tendrils can exhibit thigmonastic, traumatonastic, and thermonastic reactions. Doubtless, however, their chemonastic irritability is the main and most important one. Chemical stimuli are concerned in the movements of other insectivorous plants, *e.g. Dionaea* and *Pinguicula*.

3. Seismonasty [117]

In *Dionaea* the two halves of the leaf-blade (Fig. 217) close together not only as a result of chemical stimuli but also owing to a mechanical stimulus. In contrast to the haptotropic movements of tendrils or of *Drosera* resulting from contact with solid bodies, in the case under consideration every disturbance resulting from a mechanical shock acts as a stimulus; the movement can thus be brought about by rain-drops. These movements are termed seismonastic.

The most familiar example of seismonastic movements is furnished by *Mimosa pudica*, a tropical leguminous shrubby plant, which owes its name of sensitive plant to its extreme sensitiveness to contact.

The leaves of this plant are doubly compound (Fig. 291). The four secondary leaf-stalks, to which closely crowded leaflets are attached left and right, are articulated by well-developed pulvini with the primary leaf-stalks; while they, in turn, as well as the leaflets, are similarly provided with motile organs. Thus all these different parts are capable of independent movement, and the appearance of the entire leaf becomes, in consequence, greatly modified. In their unirritated, light position (Fig. 291, on the left) the leaf-stalk is directed obliquely upwards, while the secondary petioles with their leaflets are extended almost in one plane. Upon any vibration of

FIG. 291.—*Mimosa pudica*, with leaves in normal, diurnal position; to the right, in the position assumed on stimulation; *B*, inflorescences.

the leaf, in favourable conditions of temperature (25°-30° C.) and moisture, all its parts perform rapid movements. The leaflets fold together, and, at the same time, move forward, the secondary petioles lay themselves laterally together, while the primary leaf-stalk sinks downwards (Fig. 291, on the right). Leaves thus affected, if left undisturbed, soon resume their former position.

The behaviour of the leaves is still more remarkable when only a few of the leaflets are acted upon by the stimulus. This is easily demonstrated by holding a burning match near the leaflets of one of the pinnae. The leaflets directly affected by the flame fold quickly upwards, and this movement is performed successively by each pair of leaflets of the pinna until the articulation with the primary leaf-stalk is reached. The stimulation is then conveyed to the other pinnae, the leaflets of which go through the same movement in the

reverse order; finally, the secondary petioles themselves draw together. Suddenly, when the whole process seems apparently finished, the main leaf-stalk in turn makes a downward movement. From this leaf the stimulus is able to travel still farther through the stem, and it may thus induce movement in leaves 50 cm. distant. The stimulus can also be conducted from the roots to the leaves. In this case we are dealing with a wound-stimulus which has far-reaching effects. On otherwise disturbing the plant we also find a conduction of the stimulus which, it is true, is not so extensive.

The rate of conduction of the stimulus ([118]) may attain after wounding 10 cm. and after contact 3 cm. per second, and thus be of considerable rapidity. It is, however, greatly below the conduction of the stimulus along human nerves. While it is not yet known with certainty how the stimulus is conducted in *Mimosa*, it is clear that the process differs both from the conduction along nerves and from that in other cases in plants. The stimulus can certainly be carried across killed regions; it probably passes along the tracheides of the xylem and depends on the movement of water. *Mimosa* thus reacts not only to the stimulus of shock but to that of wounding, and the same movements of the leaves follow on electric shocks, sudden changes of temperature, and chemical stimuli.

The position of a disturbed leaf is externally similar to its sleep- or night-position, but the conditions of tension in the pulvinus which lead to the two positions differ. The seismonastic, like the sleep-position, is caused by variations in turgor, but depends on a diminution of the osmotic pressure and a flaccid condition of the half of the pulvinus that becomes concave. This condition can be most clearly recognised in the irritable under side of the main pulvinus of the leaf; it is connected with an escape of liquid from the cells into the adjoining intercellular spaces.

Many Leguminosae and Oxalideae are similar but less irritable. Thus *Robinia pseudacacia* and *Oxalis acetosella* exhibit slight movements on strong mechanical stimuli. These are much less considerable than in *Mimosa*. Movements of the leaves in response to wounding also are not confined to *Mimosa*.

The power of reaction to stimuli in *Mimosa* evidently depends on external factors, and each of these when in excess or lacking may lead to a state of rigor. Whenever the temperature of the surrounding air falls below a certain level (15°), no movements take place, and the whole plant passes into a condition known as COLD RIGOR, while, on the other hand, at a temperature of about 40°, HEAT RIGOR occurs. DROUGHT RIGOR is induced, just before withering, by an insufficient supply of water, and a DARK RIGOR by a prolonged retention in darkness. In a vacuum, or on exposure to hydrogen and other gases —chloroform vapour, coal gas, etc.—movement also ceases, partly on account of insufficient oxygen, and partly from the actual poisonous action of the gases themselves. If the state of rigor is not continued too long, the original irritability will again return on the restoration of normal conditions. Similar conditions of rigor are met with in other cases of irritability.

The variation-movements exhibited by the staminal leaves of some Berberidaceae (*Berberis, Mahonia*) and Compositae, especially beautifully by *Centaurea*

americana, bear a certain relation to those of foliage leaves. The bow-shaped filaments of the stamens of the Compositae straighten upon mechanical irritation. As they frequently contract 10-20 per cent of their length, the style becomes extended beyond the anther-tube (Fig. 292). The reduction in the length of the filaments is accompanied by a moderate increase in their thickness, due to the elastic contraction of the cell walls, and the consequent expulsion of water into the intercellular spaces. The stamens of *Berberis* and *Mahonia* are only sensitive to contact on the inner side near the base, and as their contraction occurs only on the inner side, the anthers are thus brought into contact with the stigma.

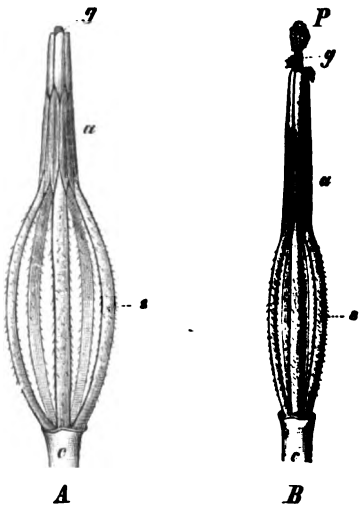


FIG. 292.—A single flower of *Centaurea jacea* with perianth removed. *A*, Stamens in normal position; *B*, stamens contracted; *c*, lower part of tubular perianth; *s*, stamens; *a*, anther-tube; *g*, style; *P*, pollen. (After PFEFFER, enlarged.)

The two lips of the stigmas of *Mimulus*, *Goldfussia*, *Martynia*, *Torenia*, and other plants close together when touched. In a short time they open and are again seismonastically sensitive. Opening also takes place when pollen has been brought to the stigma and germinated on it. The destructive effect of the pollen leads, however, to a closing movement which is not a phenomenon of irritability.

While seismonasty is a peculiar form of irritability, it is also the extreme form of haptotropism. There are plants which exhibit a perception intermediate between irritability to contact and to shock. This applies to certain etiolated seedlings, the haptotropism of which was mentioned above; a jet of water or gelatine is sufficient to stimulate them, though more weakly than stroking with solid bodies ([119]).

PART II

SPECIAL BOTANY

DIVISION I

THALLOPHYTA. BRYOPHYTA. PTERIDOPHYTA.

SPECIAL BOTANY

SPECIAL Botany is concerned with the special morphology, physiology, and ecology of plants. While it is the province of general botany to ascertain the laws that hold for the structure, vital processes, and the adaptations in the whole vegetable kingdom, it is the task of special botany to deal with the separate groups of plants. It is the endeavour of special morphology to obtain some insight into the PHYLOGENY OF THE VEGETABLE KINGDOM by morphological comparison of the manifold types of plants. The solution of this problem would provide the key for the construction of a NATURAL SYSTEM of classification of plants based upon their actual relationships. Such a system must necessarily be very imperfect, as it is not possible to determine directly the phylogenetic connection of different plants, but only to infer their relationships indirectly from morphological comparisons.

Such a natural system, founded on the actual relationship existing between different plants, stands in direct opposition to the ARTIFICIAL SYSTEM, to which has never been attributed more than a practical value in grouping the plants in such a manner that they could easily be determined and classified. Of all the earlier artificial systems, the sexual system proposed by LINNAEUS in the year 1735 is the only one which need be considered.

LINNAEUS, in establishing his classification, utilised characteristics which referred exclusively to the sexual organs, and on this basis distinguished twenty-four classes of plants. In the last or twenty-fourth class he included all such plants as were devoid of any visible sexual organs, and termed them collectively CRYPTOGAMS. Of the Cryptogams there were at that time but comparatively few forms known, and the complicated methods of reproduction of this large group of plants were absolutely unknown. In contrast to the Cryptogams, the other twenty-three classes were distinguished as PHANEROGAMS or plants whose flowers with their sexual organs could be easily seen. LINNAEUS divided the Phanerogams, according to the distribution of the sexes in their flowers, into such as possessed hermaphrodite flowers (Classes I.-XX.), and those in which the flowers were unisexual (XXI.-XXIII.). Plants with hermaphrodite flowers he again divided into three groups: those with free stamens (I.-XV.), which he further distinguished according to the number, mode of insertion, and relative length of the stamens; those with stamens united with each other (XVI.-XIX.); and those in which the stamens were united with the pistil (XX.). Each of the twenty-four classes was similarly subdivided into

orders. While some of the classes and orders thus constituted represent naturally related groups, although by the method of their arrangement in the artificial system they are isolated and widely removed from their proper position, they include, for the most part, plants which phylogenetically are very far apart.

LINNAEUS himself (1738) felt the necessity of establishing natural families in which the plants should be arranged according to their "relationships." So long, however, as the belief in the immutability of species prevailed, the expressions relationship and family could have no more than a hypothetical meaning, and merely indicated a supposed agreement between plants having similar external forms. A true basis for a natural system of classification of organisms was first afforded by the theory of evolution.

The system adopted as the basis of the following description and systematic arrangement of plants is the natural system of ALEXANDER BRAUN, as modified and further perfected by EICHLER, ENGLER, WETTSTEIN, and others.

The vegetable kingdom may be divided into the following four main groups:

1. Thallophyta.
2. Bryophyta.
3. Pteridophyta.
4. Spermatophyta.

DIVISION I

THALLOPHYTA. BRYOPHYTA. PTERIDOPHYTA

Since the time of LINNAEUS the Thallophytes, Bryophytes, and Pteridophytes have been termed collectively Cryptogams in contrast to the Phanerogams or Spermatophyta. These two main divisions are, however, of unequal systematic value, for the lower Phanerogams approach the Pteridophyta, from which they have originated, more closely than these most highly developed Cryptogams approach the Bryophyta. The Bryophyta and the Thallophyta agree in being composed of more or less uniform cells, and are contrasted as CELLULAR PLANTS with the VASCULAR PLANTS comprising the Pteridophyta and Spermatophyta. Since, however, the Bryophyta and Pteridophyta agree in many respects, and appear to have diverged from a common source, the distinction of cellular and vascular plants must not be too strongly insisted upon.

The Spermatophyta are distinguished by their distribution by means of SEEDS from the Cryptogams, which form SPORES. Spores

are unicellular structures which become separated from the parent plant, and form the starting-point of the development of a new individual. The Cryptogams might, therefore, be termed spore-bearing plants. The seed-plants also produce spores, but the sporangium and contained spore, which as a special structure develops into the seed, continues its development while still connected with the parent plant, the seeds being ultimately separated from this.

The distinctions between the Thallophytes, Bryophytes, and Pteridophytes are briefly the following:

The THALLOPHYTA include a great variety of plants, the vegetative portion of which may consist of one or many cells in the form of a more or less branched thallus. Reproduction is both sexual and asexual, but there is usually no definite succession of the two modes of reproduction. An alternation of generations only appears in the higher forms.

The BRYOPHYTA and PTERIDOPHYTA exhibit a regular alternation of two generations in their life-history. The asexual generation forms spores, and is called the SPOROPHYTE. From the spore the sexual generation or GAMETOPHYTE develops; this bears sexual organs of characteristic construction, the male organs being called antheridia, and the female organs archegonia. From the egg-cell contained in the latter, after fertilisation, the sporophyte again arises.

In the BRYOPHYTA the plant body is always a thallus, although in the higher Mosses there is a segmentation into stems and leaves. The Bryophytes possess no true roots, and their conducting bundles, when present, are of the simplest structure. The sporophyte is a stalked or unstalked capsule, which lives semi-parasitically on the sexual plant.

The PTERIDOPHYTA have small thalloid gametophytes; the sporophytes exhibit a segmentation into stems, leaves, and roots, and also possess true vascular bundles; they thus resemble the Spermatophyta in structure.

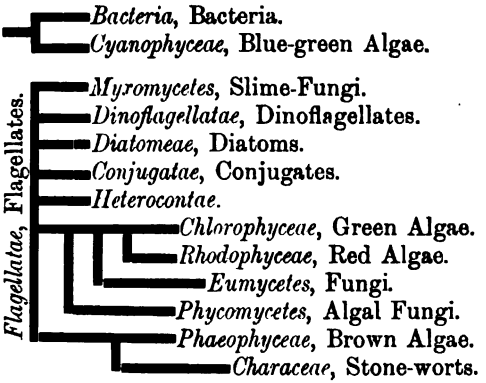
The Bryophyta and Pteridophyta are united as the Archegoniatae on account of the structural agreement in their female reproductive organs or archegonia. These organs are also present in a somewhat simplified form in the lower Spermatophyta (in most Gymnosperms), so that a sharp line cannot be drawn between the Archegoniatae and higher groups of plants.

I. THALLOPHYTA (1)

It was formerly customary to divide the Thallophyta into Algae, Fungi, and Lichens. The Algae are Thallophytes which possess chromatophores with pigments, particularly chlorophyll; they are, therefore, capable of assimilating and providing independently for their own nutrition (autotrophic). The Fungi, on the other hand, are colourless and have a saprophytic or parasitic mode

of life (heterotrophic). There are also Algae which are not strictly autotrophic but can in greater or less degree employ organic substances in their metabolism; these mixotrophic forms succeed well in impure water. Such a method of classification, however, although possessing a physiological value, has no phylogenetic significance, as it does not express the natural relationships between the various groups. In the Lichens (Lichenes), which were formerly regarded as simple organisms, the thallus affords an instance of a symbiosis of Algae and Fungi. From a strictly systematic standpoint, the Fungi and Algae composing the Lichens should be classified separately, each in their own class; but the Lichens, among themselves, exhibit such a similarity in structure and mode of life, that a better conception of their characteristic peculiarities is obtained by their treatment as a distinct class in connection with the Fungi.

The phylogenetic connections of the fourteen classes into which the Thallophyta are divided are expressed, so far as is possible, in the following scheme:



The Bacteria and Cyanophyceae are among the most simply organised Thallophyta; they are closely connected and are often grouped together as the Schizophyta. They occupy an isolated position in contrast to the remaining simple Thallophytes, which with greater or less probability may be derived from the Flagellatae. The Flagellatae used to be (and frequently still are) placed with the lowest animals. As a matter of fact they combine plant and animal characteristics, and may also be regarded as the starting-point of the lower animals. The Myxomycetes may also have sprung from them as a group of colourless saprophytes. The Peridineae are a further developed branch of the Flagellatae. The simplest forms among the Heterocontae, the Green Algae, and the Phaeophyceae connect directly with the Flagellata; on the other hand, a direct connection of the latter with the Conjugatae and Diatomeae presents greater difficulty.

The Phycomycetes have branched off from the main series of the Chlorophyceae. The origin of the Red Algae and the Eumycetes, which appear to have sprung from a common stock, is still in doubt. The Characeae occupy a quite isolated and very advanced position, and have usually been regarded as the most highly developed

of the Green Algae; they appear to be connected in important characters with the Brown Algae.

The Thallophytes are commonly multiplied and distributed by asexually produced SPORES, the mode of development of which differs in the several groups. In many cases the spores arise by a process of cell division within certain cells, which are known as SPORANGIA; in other cases they arise by modification and separation of cells of the thallus or by a process of cell-budding. When the spores possess cilia and are able to move actively in the water, they are known as swarm-spores (zoospores); when they do not bear cilia they are termed aplanospores. In the latter case the spores if distributed by water may be naked, or they may be provided with a cell wall and suited for distribution in the air.

Sexual reproduction is also of widespread occurrence. It consists, in the simplest cases, in the production of a single cell, the ZYGOSPORE or ZYGOTE, by the union or conjugation of two similarly formed sexual cells or gametes (ISOGAMY). The organs in which the gametes are formed are termed GAMETANGIA; planogametes are provided with cilia while aplanogametes are non-ciliated. In many of the more highly developed forms, however, the gametes are differentiated as small, usually ciliated, male cells or SPERMATOZOIDS, and as larger non-ciliated female cells, the egg-cells or OOSPHERES. The spermatozoids are formed in ANTHERIDIA, the oospheres in OOGONIA. The zygote which results from the fertilisation of an oosphere by a spermatozoid is known as an OOSPORE when it passes into a resting condition; it may, however, in certain groups commence its development at once. It must be assumed that the sexual cells have been derived in the phylogeny of plants from asexual spores. The gametangia, oogonia, antheridia, and sporangia of the Thallophyta are homologous structures. The sexual reproduction has originated independently in several distinct groups.

While the reproduction of some Thallophyta is exclusively asexual, and of others exclusively sexual, in many others both forms of reproduction occur. In the latter case this may occur on the one plant, or separate successive generations may be distinguishable. Generally speaking, there is, however, no regular succession of asexual and sexual generations in Thallophytes, the mode of reproduction being to a great extent under the influence of external conditions (²). Only in some Brown Sea-weeds, in the Red Sea-weeds, and some Fungi is there an alternation of a sexual generation (gametophyte) with an asexual (sporophyte), such as is found in all Bryophytes and Pteridophytes.

In the union of the two sexual cells the fusion nucleus obtains the double number of chromosomes; it becomes DIPLOID while the sexual cells always have HAPLOID nuclei. A REDUCTION DIVISION of the diploid nucleus to the haploid must therefore occur in the course of the ontogenetic development and a distinction can thus be made between a haploid and a diploid phase in the life-history of the plant. The reduction division in many groups of Thallophyta takes place in the germinating zygote. It may, however, occur at different stages even in the

same natural group and is thus not necessarily connected with the commencement of a new generation. In certain Brown Algae and in all Archegoniatae the reduction takes place in the sporangia so that the gametophyte is regularly haploid and the sporophyte diploid. The nuclear difference cannot, however, be regarded as determining the specific structure of the alternating generations.

The reproductive cells (swarm-spores, gametes) of the classes of Thallophyta which can be derived from the Flagellata are in many cases ciliated, naked protoplasts resembling the cells of Flagellates. Even in the Bryophyta and Pteridophyta, and also in the Cycadeae and Ginkgoaceae, the male gametes, though also secondarily modified, exhibit this return during the ontogeny to the phyletic original form.

Class I

Bacteria [1, 3-9]

Bacteria are unicellular or filamentous organisms of very simple construction. Chlorophyll is wanting in them, and their mode of life is usually a parasitic or saprophytic one. A large number of species exist distributed over the whole earth, in water, in the soil, in the atmosphere, or in the bodies of dead or living plants and animals. They are often termed Fission Fungi, or Schizomycetes, since the multiplication of the unicellular forms takes place by a division into two and the separation of the segments. This mode of multiplication is also found in other unicellular plants.

The cells of the Bacteria are surrounded by a thin chitinous membrane, and contain a protoplasmic body, which is usually colourless, and can be made to contract away from the membrane by plasmolysis. The protoplasm may contain one or more vacuoles. One or several granular structures are also present in the protoplast; these so-called chromatin bodies may be deeply coloured by stains, and have been regarded as nuclei by various authors. Since, as yet, undoubted karyokinetic division has not been observed in these bodies, the presence of nuclei in the bacterial cell cannot be regarded as certainly established.

For the most part the Bacteria are extraordinarily minute organisms, and probably include the smallest known living beings. The spherical cells of the smallest forms are only 0·0008 mm. in diameter; the rod-shaped cells of the tubercle bacillus are only 0·0015-0·004 mm. long, while most species are about 0·001 mm. broad and 0·005 mm. long.

The simplest forms of Fission Fungi are minute spherical cells, COCCI. Forms consisting of rod-shaped cells are designated BACTERIUM or BACILLUS. Rod-shaped forms with a slight spiral curvature are called VIBRIO, and those more strongly curved SPIRILLUM. The unicellular cocci, rod-shaped forms, and vibrios may also remain united in chains after the cell division. Frequently the cell membranes

undergo a mucilaginous swelling, the cells or cell-rows being embedded in the gelatinous mass. This stage of development is termed ZOOGLOEA.

In contradistinction to these unicellular HAPLOBACTERIA the TRICHOBACTERIA form filaments which as a rule are simple (*Leptothrix*, *Beggiatoa*, *Crenothrix*). In *Cladothrix*, however, they exhibit what is termed false branching. This comes about by the distal portion of the filament being left on one side while the original line is continued by the division of the cell behind the break.

Many Bacteria are motile. Their independent movements are due to the vibration and contraction of fine protoplasmic cilia ([8a]). These cilia, according to A. FISCHER, are either distributed over the whole surface of the cells (peritrichous) (*e.g. Bacillus subtilis*, Fig. 295 *a*, *d*; *Bacillus typhi*, Fig. 293 *c*; *Bacillus tetani*, Fig. 298 *e*), or

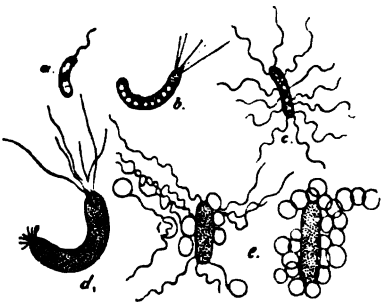


FIG. 293.—Types of arrangement of flagella. *a*, *Vibrio cholerae*; *b*, *d*, *Spirillum undula*; *d*, development of a new bunch of cilia in division; *c*, *Bacillus typhi*; *e*, *Bacillus subtilis*. (× 2250. After A. FISCHER.)

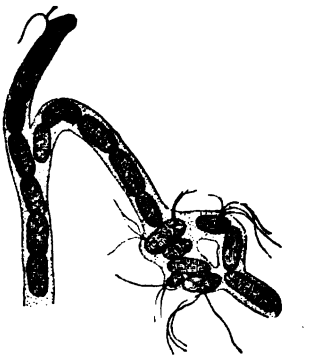


FIG. 294.—*Cladothrix dichotoma*. Formation of swarm-cells from the cells of the filament. (× 1000. After A. FISCHER.)

they spring from a single point either as a single flagellum (monotrichous) or as a group (lophotrichous). A single, polar flagellum occurs in *Vibrio cholerae* (Fig. 293 *a*); a polar terminal tuft of flagella in *Spirillum undula* (Fig. 293 *b*, *d*); a lateral tuft in the swarm-spores of *Cladothrix* (Fig. 294). The ciliary tufts may become so closely intertwined as to present the appearance of a single thick flagellum. The cilia are never drawn within the body of the cell, but undergo dissolution before the formation of spores takes place, or under unfavourable conditions (Fig. 293 *e*).

Multiplication of the individual is accomplished vegetatively by the active division or fission of the cells; the preservation and distribution of the species by the asexual formation of resting spores. These arise as endospores (Figs. 295 *c*, 296 *e*, *f*) in the middle or at one end of a cell by the inner portion of the protoplasm separating itself from the peripheral, and surrounding itself with a thick membrane. The membrane of the mother cell becomes swollen and

disintegrated when the spore is ripe. Spores are not found in all species.

Order 1. Haplobacteria. Unicellular Bacteria

This includes the great majority of the species.

Although the cycle of forms passed through in the life-history of a Bacterium is a very simple one, the individual species, which can often be barely distinguished by morphological characters, show great variety in their metabolic processes and in their mode of life. The majority of Bacteria require oxygen for their respiration, and are therefore aerobic; many can, however, develop without this gas, while some species, *e.g.* the butyric acid bacterium and the tetanus bacillus, are strictly anaerobic and only succeed in the absence of oxygen. Some bacteria produce by their respiration considerable heat; this is the explanation of the spontaneous heating of damp hay, dung, tobacco, and cotton-wool. In such substrata *Bacillus calfactor* develops; it is adapted to live at high temperatures (above 40°) and is still motile at over 70° C. (cf. p. 277).

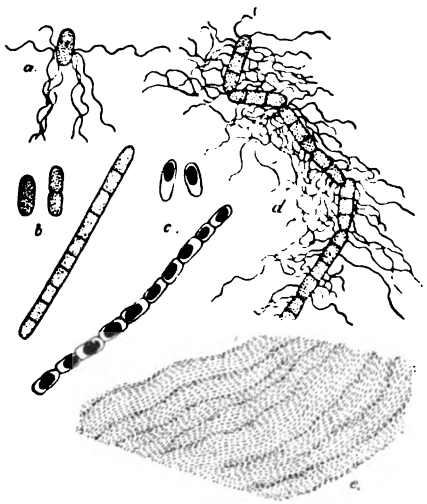


Fig. 295.—*Bacillus subtilis*. *a*, *d*, Motile cells and chain of cells; *b*, non-motile cells and chains of cells; *c*, spores from the zoogloea, *e*. (*a-d* × 1500; *e* × 250. From A. Fischer, *Vorles. über Bacterien.*).

Saprophytic and parasitic species are distinguished, although a sharp separation is often impossible. In cultures the parasitic forms can be made to lead a saprophytic life on suitable substrata.

Bacillus subtilis, the Hay bacillus (Fig. 295), which appears as a rule in the decoction obtained by boiling hay in water, will afford an example of the life-history of a bacterium. The spores of this species, which withstand the effect of the boiling water, produce on germination rod-shaped swarming cells with cilia on all sides; these divide and may remain connected in short chains. At the surface of the fluid these swarming cells change into non-motile cells without cilia; these divide up, giving rise to long intertwined chains of cells. These are associated together in the pellicle covering the surface (zoogloea stage). Spore formation occurs when the nutritive substances in the fluid are exhausted.

The zymogenous or fermentation Bacteria and the saprogenous or decomposition Bacteria are other saprophytic forms. The former oxidise or ferment carbohydrates. The latter decompose nitrogenous animal or vegetable substances (albumen, meat, etc.) with the liberation of ill-smelling gases.

The acetic acid bacteria (Fig. 296 *a*, *b*, *c*) oxidise alcohol to acetic acid. The transformation of sugar into lactic acid is brought about by the rod-like cells of *Bacillus acidi lactici* (Fig. 296 *d*). *Clostridium butyricum* (Fig. 296 *e*) forms butyric acid from various carbohydrates in the absence of oxygen, while certain

marsh bacteria (Fig. 296 *f*) in the absence of oxygen form marsh-gas and hydrogen from cellulose. *Bacillus proteus* is the most common cause of decomposition of meat, albumen, etc.

Streptococcus (*Leuconostoc*) *mesenterioides* (Fig. 297) causes fermentation of beet-sugar. It forms large mucilaginous masses like frog-spawn, the bead-like rows of cells being surrounded by a gelatinous investment. The latter is not formed in media from which sugar is absent.

The Purple Bacteria, which develop in water containing decomposing organic matter in the absence of oxygen and the presence of light, contain, according to MOLISCH (4), a green and a red pigment (bacterio-chlorin and bacterio-purpurin). Other bacteria secrete pigments in their cells or around them. The latter is the case with *Bacillus prodigiosus*, the ellipsoid peritrichous rod-shaped cells of which form fuchsin-red colonies on milk or bread, and so have given rise to the miracle of the bleeding Host.

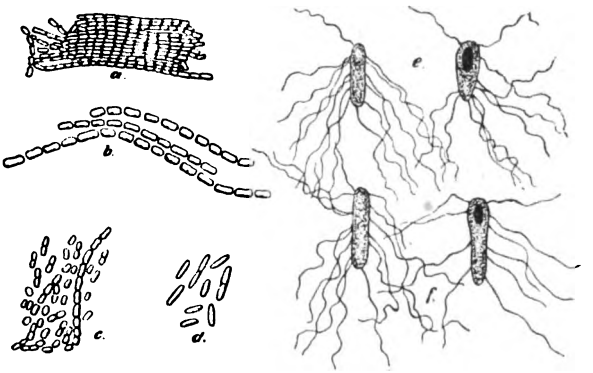


FIG. 296.—Bacteria of fermentation. *a-c*, Vinegar bacteria; *a*, *Bacillus aceti*; *b*, *Bac. Pasteurianus*; *c*, *Bac. Kutzingianus*; *d*, *Bac. acidi lactici*, lactic acid bacillus; *e*, *Clostridium butyricum*, butyric acid bacillus; *f*, *Plectridium paludosum*, fermentation bacterium from marsh water. (× 1000. From A. FISCHER, *Vorles. über Bacterien.*)

The photogenic bacteria produce within their cells a substance which becomes phosphorescent on oxidation. The most widely spread of these phosphorescent bacteria (5) is *Bacterium phosphoreum*, which occurs on meat.

Certain soil-bacteria (*Clostridium Pasteurianum*, *Azotobacter chroococcum*) and marine bacteria are able to assimilate free nitrogen. To these nitrogen-fixing forms also belong *Bacillus* (*Rhizobium*) *radicicola* and *Bacillus Beijerinckii* which live symbiotically in the root-nodules of the Leguminosae (Figs. 251, 252). *Mycobacterium Rubiacearum* is similarly symbiotic in the leaves of tropical Rubiaceae and produces analogous bacterial galls (6). On the other hand, de-nitrifying bacteria, which decompose nitrates and nitrites with liberation of free oxygen, occur both in the soil and in the sea (cf. p. 276).

The parasitic bacteria inhabit both animals and plants causing bacterioses. *Bacillus tumefaciens*, discovered by Smith, gives rise to the cancer-like tumours of Crown-gall on the higher plants. This organism is also pathogenic to man. Another example is *Bacillus phytophthorus*, which attacks the potato (7).

The numerous pathogenic Bacteria are the most important causes of infectious diseases. Their injurious influence on the tissues and blood of men and animals

is brought about by the excretion of poisonous substances, to which the name toxins has been given. The following forms may be mentioned. *Staphylococcus pyogenes* (Fig. 298 *a*), the cocci of which form irregular or racemose masses, is the most common cause of suppuration, while *Streptococcus pyogenes* (Fig. 298 *b*), with cocci united in chains, occurs in erysipelas and other suppurative lesions. *Micrococcus* (*Diplococcus*) *gonorrhoeae* (Figs. 298 *c*, 299 *a*) has somewhat flattened cocci arranged in pairs, and causes gonorrhoea. *Bacillus anthracis* (Figs. 298 *d*, 299 *c*) was found by R. KOCH in the blood and organs of animals suffering from splenic fever. The relatively large rod-shaped cells may be united in short chains; they form endospores in cultures in the same way as the Hay bacillus. *Bacillus tetani* (Fig. 298 *e*) occurs in the soil, and is the cause of tetanus. Its straight rod-shaped cells are ciliated, and grow only in the wound itself; their spores are formed in the swollen end. *Bacillus influenzae*, short, slender rods; *Bacillus pestis*, small, stout, non-motile rods. LÖFFLER'S *Bacillus diphtheriae* (Fig. 298 *f*) consists of small rod-shaped cells sometimes thickened at one end. KOCH'S *Mycobacterium tuberculosis* (Figs. 298 *g*, 299 *b*), which is found in all tuberculous lesions and secretions, and in the sputum, is a slender, slightly curved rod; branched forms also occur. It is non-motile and does not form spores. For

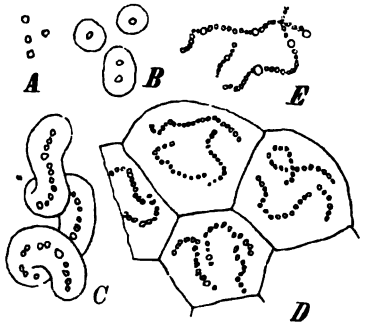


FIG. 297.—*Streptococcus mesenterioides*. *A*, Isolated cells without gelatinous sheath; *B*, *C*, formation of chain of cells with gelatinous sheath; *D*, portion of mature zoogloea; *E*, formation of isolated cells in the filaments of the zoogloea. (× 520. After VAN TIEGHEM.)

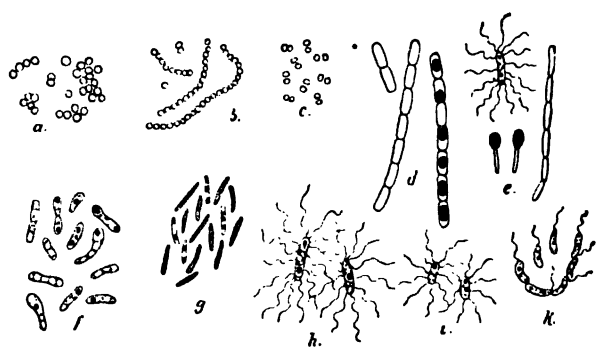


FIG. 298.—Pathogenic Bacteria. *a*, Pus cocci; *b*, erysipelas cocci; *c*, gonorrhoea cocci; *d*, splenic fever bacilli; *e*, tetanus bacilli; *f*, diphtheria bacilli; *g*, tubercle bacilli; *h*, typhoid bacilli; *i*, colon bacilli; *k*, cholera vibrios. (× about 1500. From A. FISCHER, *Vorles. über Bacterien*.)

these reasons it is grouped with some other species in a special family, the Mycobacteriaceae (8). Typhoid fever is caused by the ciliated cells of *Bacillus typhi* (Fig. 298 *h*); *Bacillus coli* (Fig. 298 *i*), the colon bacillus, which is as a rule harmless and always occurs in the human intestine, closely resembles the typhoid bacillus. The comma bacillus of Asiatic cholera, *Vibrio cholerae* (Fig. 298 *k*),

was discovered by R. KOCH. It occurs in the intestine as short curved rods with a single polar flagellum, and sometimes in longer spirally-wound chains.

a *b* *c*

FIG. 299.—Stained preparations from Ziegler's *Text-book of Pathology*. *a*, Gonococci in the gonorrhoeal discharge, mucus and pus corpuscles with cocci (methylene blue and eosin), × 700; *b*, tubercle bacilli in sputum of phthisis (fuchsin and methylene blue), × 400; *c*, splenic fever bacilli in the pustule of the disease (methylene blue and vesuvin), × 350. (From A. FISCHER, *Vorles. über Bacterien.*)

Besides the above injurious parasites there are others which are more or less harmless occurring on the mucous membranes, in the mouth (Fig. 80), or the intestine. *Sarcina ventriculi*, which occurs as packets of cocci in the stomach and intestine of man, will serve as an example of these.

In addition to saprophytic and parasitic Bacteria, there are others which, though possessing no chlorophyll, obtain their food from inorganic compounds only. These are the Nitrite Bacteria (*Nitrosomonas*) and the Nitrate Bacteria (*Nitrobacter*), which live in the soil. The former oxidises ammonia to nitrous acid, and the latter oxidises the nitrous to nitric acid. They both obtain their carbon from carbonic acid, and thus derive their food independently of any organic food-supply (Fig. 300, cf. p. 254).

a. *b.* *c.*

FIG. 300.—Nitrifying bacteria, after WINOGRADSKY. *a*, *Nitrosomonas europæa*, from Zurich; *b*, *Nitrosomonas javanensis*, from Java; *c*, *Nitrobacter*, from Quito. (× 1000. From FISCHER, *Vorles. über Bacterien.*)

Order 2. Trichobacteria. FILAMENTOUS BACTERIA (9)

The filamentous bacteria comprise only a few genera. They approach in their organisation the filamentous Cyanophyceae and may, in part at least, have been derived from these as colourless forms. The majority live saprophytically in water but some are autotrophic.

The widely distributed *Cladothrix dichotoma* is morphologically the highest among these. It is found in stagnant water, and consists of falsely-branching

delicate filaments attached to Algae, stones, and woodwork, and forming a slimy coating over them ; the filaments are composed of rod-shaped cells. Reproduction is effected by ciliated swarm-cells, which originate by division from cells of the filament and are set free by the swelling of the sheath (Fig. 294). The swarm-cells come to rest after a time and grow into new filaments.

Another very common form is *Crenothrix polyspora*, which consists of unbranched filaments attached to the substratum, but easily broken, and can accumulate hydrated oxide of iron in its sheaths. It often forms masses in the cavities of water-pipes, blocking them up and rendering the water undrinkable. The reproduction of *Crenothrix* is effected by small, round, non-motile cells, which arise by subdivision of the cells of a filament enclosed by its sheath.

The numerous kinds of Sulphur Bacteria, of which *Beggiatoa alba* is the most widely distributed, are found in sulphurous springs and at the bottom of pools where sulphuretted hydrogen is being formed by decomposition of organic material. The sulphur bacteria can thus live autotrophically, without organic food, utilising in their metabolism salts of ammonium and carbon dioxide. These bacteria oxidise sulphuretted hydrogen into sulphur, and store the latter substance in the form of rounded granules within their cells, ultimately oxidising it to sulphuric acid. Some Haplobacteria also belong to this physiological group (cf. p. 276).

Chlamydothrix (*Leptothrix*) *ochracea*, the so-called Iron-Bacterium, oxidises oxide of iron to the hydrated oxide of iron which it accumulates in the sheaths of its filaments. It occurs in ditches and swampy places in meadows. It can thus exist with only a trace of organic food, but on the other hand succeeds well without iron in organic food-solutions.

Other iron-bacteria such as *Spirophyllum ferrugineum* according to LIESKE are purely autotrophic. They only succeed in water containing in addition to small quantities of inorganic salts some carbonate of iron. They oxidise the ferrous oxide to the hydrated oxide of iron which they accumulate. This oxidation process supplies the energy for the assimilation of carbon dioxide.

CLASS II

Cyanophyceae, Blue-green Algae ([1, 10])

The Cyanophyceae are simply organised unicellular or filamentous Thallophytes of a bluish-green colour ; the cells or filaments are frequently united into colonies by the gelatinous swelling of the cell walls. The numerous species, which are distributed over the earth, live in water, or form gelatinous or filamentous growths on damp soil, damp rocks, or the bark of trees. Like the pure green Algae, they are autotrophic.

The protoplast of each cell possesses a peripheral chromatophore of the form of a hollow cylinder or hollow sphere ; in addition to chlorophyll this contains a blue-green pigment (phycocyan) from which the name of the class is derived, and in some species also a red pigment (phycoerythrin). The product of assimilation is glycogen. The centre of the cell is occupied by the colourless central body, which corresponds to a nucleus and contains chromosome-like structures. As definite inclusions of the cells may be mentioned the cyanophycin granules,

which are of proteid nature and are situated within the chromatophore. The cell wall consists of cellulose and pectic substances.

Reproduction is exclusively vegetative by cell division. In many forms resting spores arise by the enlargement of single cells, the walls of which become greatly thickened (Fig. 302). This process differs from that in the Bacteria.

Just as the Bacteria are designated Fission Fungi (Schizomycetes), the Blue-green Algae may be termed Fission Algae (Schizophyceae), since the reproduction of both depends on fission. The two groups would form the class of fission plants Schizophyta. The Bacteria and the Cyanophyceae have much in common, but the cilia and endospores of the former are unknown in the latter group.

The simplest Cyanophyceae consist of spherical cells; this is the case with species of *Chroococcus*. In *Gloeocapsa* (Fig. 35), found on damp rocks and walls,

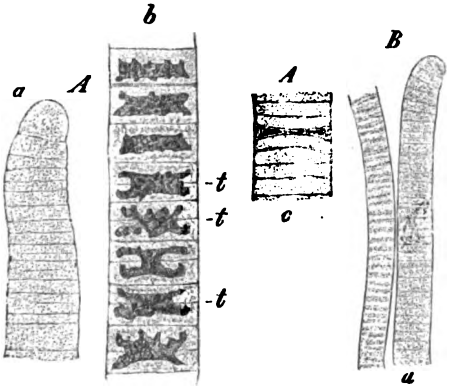


FIG. 301.—*A*, *Oscillaria princeps*: *a*, terminal portion of a filament; *b* and *c*, portions from the middle of a filament properly fixed and stained; *t*, cells in division (× 1080). *B*, *Oscillaria Froelichii* (× 540). (After STRASBURGER.)

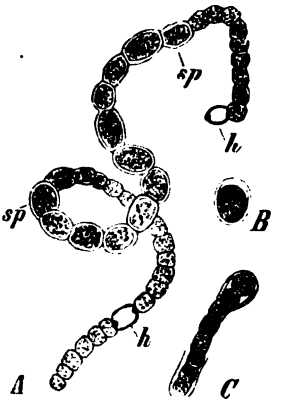


FIG. 302.—*Nostoc Linckii*. A species that floats freely in water. *A*, Filament with two heterocysts (*h*) and a large number of spores (*sp*); *B*, isolated spore beginning to germinate; *C*, young filament developed from spore. (× 650. After BORNET.)

the cells remain connected together after division in a gelatinous mass, forming a multicellular colony.

The species of *Oscillaria*, which occur everywhere in water or on damp soil, are the simplest of the filamentous forms which may be unbranched or exhibit false branching (Fig. 86). The filament, which is usually provided with a thick sheath, consists of similar flattened cells (Fig. 301). It can separate into pieces (hormogonia), which become free owing to the pressure of the sheath, and grow into new filaments. In other filamentous Cyanophyceae specially modified cells with their contents degenerated occur in the filament. The significance of these HETEROCYSTS is not yet clear. The species of *Nostoc* (Fig. 302), whose bead-like filaments are united by the swelling of the cell walls into more or less spherical gelatinous colonies living on damp soil or in water, afford an example of this.

The filamentous Cyanophyceae, especially the Oscillarieae and the hormogonia of *Nostoc* and some related genera carry out creeping movements on a solid

substratum and are both phototactic and chemotactic. These movements are effected by the swelling of an anisotropous mucilage excreted by the cells. The main axis of swelling of this forms an acute angle with the long axis of the filament, so that the latter is moved forwards without rotating on its axis [10a].

Some Cyanophyceae take part with the Fungi in the formation of Lichens. Some species also are endophytic and inhabit cavities in other plants, *e.g.* *Anabaena* in *Azolla*, *Nostoc* in some Liverworts, in *Lemna*, and in the roots of *Cycas*. *Nostoc punctiforme* occurs as a facultative parasite in the rhizome of *Gunnera* [10b].

Class III

Flagellata (Flagellates) [1, 11, 12]

The Flagellata are a group of unicellular, aquatic organisms exhibiting a wide range of form; they combine animal and vegetable characteristics, and may be regarded as the starting-point on the one side of unicellular Thallophytes, on the other of the Protozoa.

The protoplast exhibits contractile or amoeboid movements, and is limited by a denser protoplasmic layer and not by a definite cell wall. One or more cilia (flagella) are present as motile organs. The protoplast contains a nucleus, a pulsating vacuole, and in many species well-formed green, yellow, or brownish-yellow chromatophores. A red eye-spot is frequently present. The assimilation product is usually oil, but starch and other carbohydrates also occur. Other forms are colourless and are saprophytic or obtain their food like animals. The protoplast of some Flagellates, especially of the colourless forms,

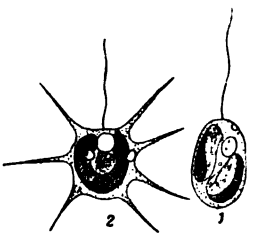


Fig. 303.—*Chrysamoeba radians*. Occurs in fresh water and has a single cilium and two brownish-yellow chromatophores. *1*, Ordinary form; *2*, amoeboid condition with radiating pseudopodia. (After Klebs.)

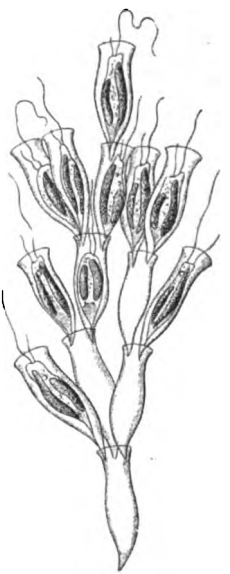


Fig. 304.—*Dinobryon Sertularia*. Occurs in fresh-water plankton and forms invested colonies. (× 600. After Senn.)

may take on an amoeboid condition in which it exhibits changes in form and creeping movements. In other cases slender processes or pseudopodia may be put out and again withdrawn as in the Rhizopoda. These assist in the absorption of solid particles of food (Figs. 303, 309).

Most representatives of the group live as naked, free cells; others form more or less complicated cell-colonies held together by mucilage, or they possess peculiar stalked or unstalked firm investments sometimes with siliceous or calcareous skeletal structures.

Sexual reproduction is wanting. Multiplication takes place by longitudinal division, and in many species thick-walled resting spores or cysts are produced. On the germination of these, after division of the contents, a number of daughter cells may be liberated (Fig. 308 *B*).

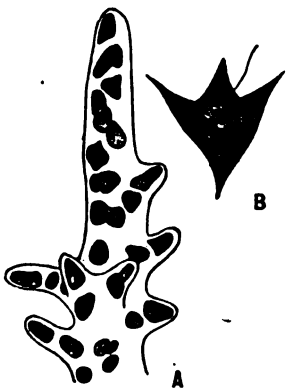


FIG. 305.—*Hydrurus foetidus*. *A*, Apex of a branch of the colony enclosed in mucilage. (After BERTHOLD.) *B*, Swarm-cell. (After KLEBS.) (From PASCHER, *Flagellaten*.)

The **Chrysomonadinae** are an important group of the Flagellata, to which belong *Chrysamoeba* (Fig. 303) and the colonial form, *Dinobryon* (Fig. 304). They are characterised by their radial structure and by their chromatophores which are usually brownish yellow, less commonly red or blue green, and form a special carbohydrate

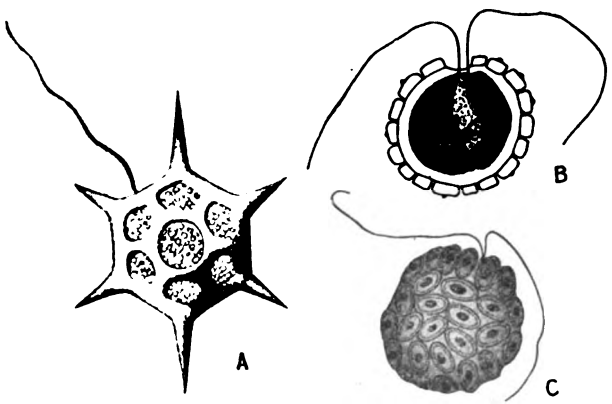


FIG. 306.—*A*, *Distephanus speculum*. (After BORGERT.) *B*, *C*, *Calyptrosphaera insignis* from the Adriatic; *B* is in optical section and *C* in surface view. (× 1600. After SCHILLER.)

(leucosin). *Hydrurus foetidus* (Fig. 305) is an example of a more complex member of the Chrysomonadinae. Its cells are associated in colonies as long branched mucilaginous filaments which may be 30 cm. in length and are attached to stones in running water. Numerous cells without cilia are embedded in the

mucilage of the filament and increase in number by longitudinal division. From these are derived uniciliate swarm-cells, which escape from the filament and ultimately become attached and produce new filaments. In other related Flagellates also such alga-like resting stages predominate, while the motile cells serve for reproduction and dispersal. Two peculiar families of small organisms found in the plankton of the sea can be placed along with the Chrysomonadinae. These are the **Silicoflagellatae** [12e] which have perforated siliceous skeletons (Fig. 306 *A*) and the **Coccolithophoroideae** [12b] which have a wall composed of calcareous plates or rods and reproduce by producing usually four swarm-spores (306 *B*). The Diatomeae and the Heterocontae appear to have been derived from the neighbourhood of the Chrysomonadinae, so that these three groups might be associated together as the Chrysophyta.

The **Cryptomonadinae** are rather more highly organised than the Chrysomonadinae and differ from them in the dorsiventral protoplast obliquely truncated at the anterior end where two cilia of unequal length arise from a depressed furrow (Fig. 307). *Chrysidella* (*Zooxanthella*) belongs to this group. They are symbiotic with various marine animals (Radiolariae, Actiniae, etc.), in the protoplasm of the cells of which their yellow resting cells lie. From these the protoplast later emerges in the form of a ciliated Flagellate. The Dinoflagellatae are related to the Cryptomonadinae. Some other genera, such as *Phaeocystis* and *Phaeothamnion* which form mucilaginous colonies during most of their life, may also be placed here. They suggest comparison with the Brown Algae, but it is doubtful whether they should be regarded as really leading to that group.

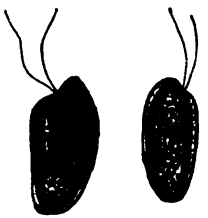


FIG. 307.—*Cryptomonas erosa*. (× 650. After STEIN.)

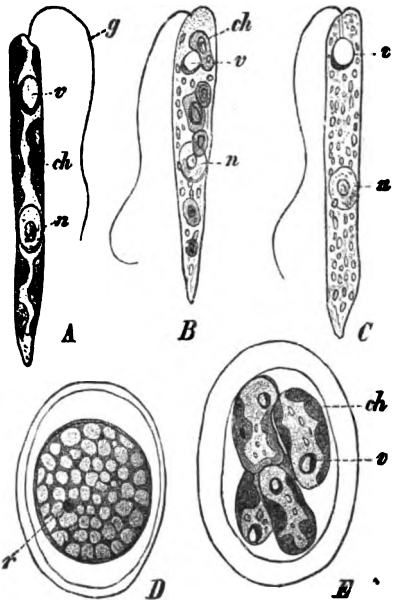


FIG. 308.—*Euglena gracilis*. *A*, Form with green chromatophores (*ch*); *n*, nucleus; *v*, vacuole and red eye-spot; *g*, flagellum. *B*, Hemi-saprophytic form with small green chromatophores. *C*, Colourless saprophytic form occurring in nutrient solution in absence of light. *D*, Resting cyst of the form *C*; *r*, red eye-spot. *E*, Germination of the resting cyst of the form *A* by division into four daughter cells which later escape. (*A*, *C* × 630; *B* × 650; *D*, *E* × 1000. After ZUMSTEIN.)

The starting-point of the Chlorophyceae is to be looked for among the Flagellates provided with green chromatophores.

The **Euglenineae** [12e] are an advanced group of green Flagellates. Species of *Euglena* (Fig. 308 *A*) often form a green scum on ponds. There are nearly allied but colourless saprophytic forms. *Euglena gracilis* can indeed be changed into a

hyaline form with leucoplasts when cultivated in organic solutions in the dark. Sexual reproduction has been observed by GERTRAUD HAASE in *Euglena sanguinea*,

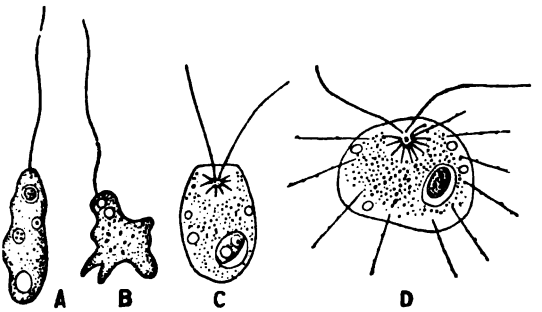


FIG. 309.—*Mastigamoeba invertens*. *A*, Free swimming. *B*, Amoeboid condition. (× 1083.) *Dimorpha mutans*, with retracted (*C*) and extended (*D*) pseudopodia. An ingested particle of food is within a vacuole. (× 666. After LEMMERMANN.)

but this requires confirmation. It takes place in the spring at the bottom of the pool, the cells throwing off their flagella and dividing into small amoeboid gametes with one nucleus and two chromatophores; these gametes then conjugate in pairs. The zygote without undergoing a period of rest then divides into four or eight cells which grow into the normal individuals.

The numerous colourless Flagellates which have saprophytic or animal-like nutrition must have been derived from those with coloured chromatophores. In some cases near relationship is indicated by agreement in the structure of the cells.

In the **Pantostomatineae** particles of food are ingested over the whole surface by means of pseudopodia (Fig. 309), in the **Protomastiginae** usually at an oral opening, while two such spots are present in the **Distomatineae**. To the second group belong certain forms that live in the blood and the gut of animals and give rise to some tropical diseases. Thus *Trypanosoma Brucei* causes the Tsetse-disease of cattle, and *T. gambiense* (Fig. 310) the sleeping sickness in man; both are conveyed by flies belonging to the genus *Glossina*.

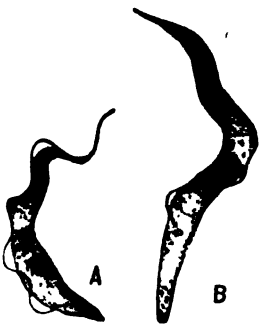


FIG. 310.—*Trypanosoma gambiense*. *A*, From the blood of an infected monkey, the flagellum forming an undulating membrane. *B*, From the fly *Glossina* with the flagellum internal. (After MINCHIN.)

It may be assumed that the Myxomycetes arose from colourless Flagellates and also that the lower Protozoa (Rhizopoda) can be placed in relation to them as a lower group.

CLASS IV

Myxomycetes (Slime Fungi) [1, 13, 14, 15]

The Myxomycetes form an independent group of lower Thallophytes; in certain respects they occupy an intermediate position between plants

and animals, and have in consequence also been termed Mycetozoa or Fungus-animals. They are represented by numerous species, and are widely distributed over the whole earth. In the first instance the behaviour of the most comprehensive Order, the **Myxogasteres**, may be considered. In their vegetative condition these Slime Fungi consist of naked masses of protoplasm, the PLASMODIA, containing numerous small nuclei but utterly devoid of chlorophyll. Glycogen occurs as a reserve substance, while starch is not found. The plasmodia (Fig. 4) are found most frequently in woods, upon soil rich in humus, upon fallen leaves, and in decaying wood. They creep about on the substrata, changing their form at the same time, and thrust out processes or pseudopodia, which may in turn coalesce. They feed by taking up solid particles and reach favourable situations for their nutrition owing to their capacity of chemotactic, hydrotactic, and negatively phototactic movements. At the period of spore-formation the plasmodium creeps out from the substratum towards the light and air, and, after coming to rest, is converted into a single or into numerous and closely contiguous fructifications, according to the genus. On the periphery of each fructification an outer envelope or PERIDIUM is formed; while internally the contents of the fructification separate into SPORES, each of which is provided with a nucleus, and enclosed by an outer wall. In many genera, part of the internal protoplasm within the SPORANGIUM or spore-receptacle is utilised in the formation of a CAPILLITIUM (Figs. 311 *A*, *B*, 312 *B*), consisting of isolated or reticulately-united threads or tubes. Upon the maturity of the spores, the peridium of the sporangium becomes ruptured, the capillitium expands (Fig. 311 *B*), and the spores are dispersed by the wind, aided by the hygroscopic movements of the capillitium. In the case of the genus *Ceratiomyxa*, the process is somewhat simplified, as the fructification is not enveloped by a peridium, and the spores are produced on the surface at the ends of short stalks.

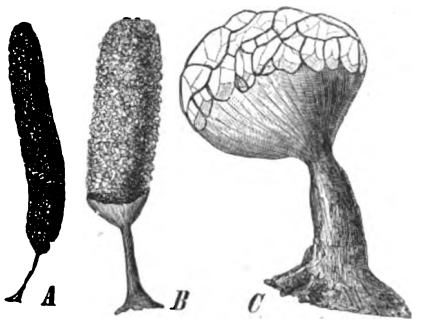


FIG. 311.—Ripe fructifications, after discharge of the spores. *A*, *Stemonitis fusca* (× 10); *B*, *Arcyria punicea* (× 12); *C*, *Cribraria rufa* (× 32).

The germination of the spores (Fig. 313, *Chondrioderma*) takes place in water or on a wet substratum. The spore wall is ruptured and left empty by the escaping protoplast. After developing a flagellum or CILIUM as an organ of motion, the protoplast swims about in the water, being converted into a SWARM-SPORE (Fig. 313 *e-g*) which resembles certain Flagellata, with a cell-nucleus in its anterior or ciliated end, and a contractile vacuole in the posterior end of its body. Even within the

spore a division may take place, so that two swarm-spores are liberated. In some species the swarm-spores can increase in number by fission. Eventually the

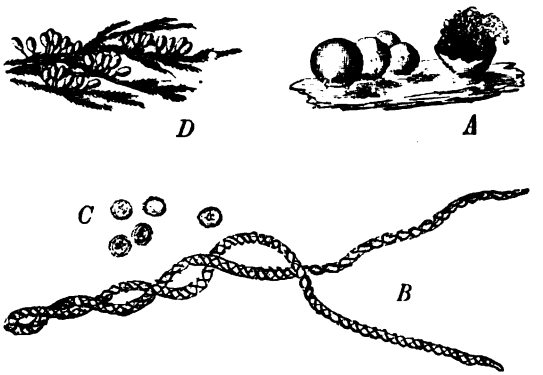


FIG. 312.—*Trichia varia*. *A*, Closed and open sporangia (× 6); *B*, a fibre of the capillitium (× 240); *C*, spores (× 240). *D*, *Leocarpus fragilis*. Groups of sporangia upon a Moss. (Nat. size.)

cilium is drawn in, and the swarm-spore becomes transformed into a MYXAMOEBA (Fig. 313 *i*, *k*); these have the capacity of multiplication by division (Fig. 314 *A*, *B*). In conditions unfavourable for their development they surround themselves with walls, and as MICROCYSTS pass into a state of rest, from which, under favourable

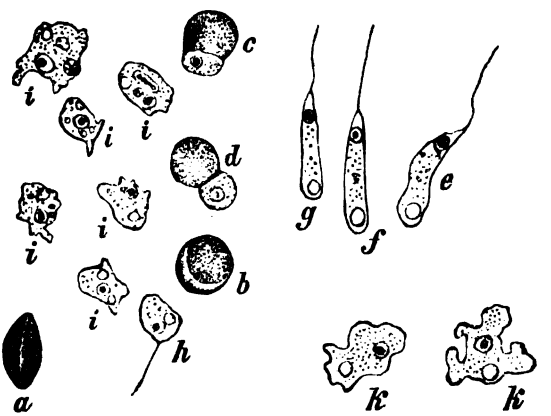


FIG. 313.—*Chondrioderma difforme*. *a*, Dry, shrivelled spore; *b*, swollen spore; *c* and *d*, spores showing escaping contents; *e*, *f*, *g*, swarm-spores; *h*, swarm-spore changing to a myxamoeba; *i*, younger, *k*, older myxamoebae. Cf. Fig. 4. (× 540. After STRASBURGER.)

conditions, they again emerge as swarm-spores. According to JAHN [14] the myxamoebae fuse in pairs, their haploid nuclei uniting (Fig. 314 *C*).

The uninucleate amoeboid zygotes, which have thus resulted from a sexual fusion, unite to form larger multinucleate plasmodia. These take up additional

haploid amoebae, but these are digested within vacuoles (Fig. 314 *D*). Ultimately the plasmodium proceeds to form the fructification. The diploid nuclei of the plasmodium undergo repeated mitotic divisions (Fig. 314 *E*). Their last division shortly before the delimitation of the spores is a heterotypic division, in which the chromosomes are reduced to the half number. Each haploid nucleus thus formed becomes the nucleus of a spore. The nuclei not employed in spore-formation degenerate. In *Ceratiomyxa* the spores may include a degenerating nucleus as well as the normal one. From the latter by two successive divisions four nuclei are formed and are present in the ripe spore. Another division occurs on germination, so that ultimately eight swarm-spores are produced from each spore.

In the structure of their swarm-spores and myxamoebae the Myxomycetes show their derivation from organisms of the nature of the Flagellata. Plasmodial fusions are also known among Flagellates.

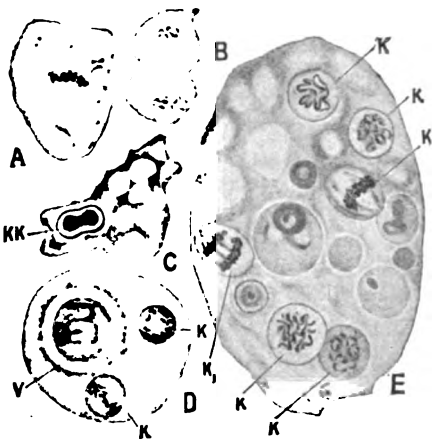


FIG. 314.—*Physarum didermoides*. *A*, *B*, Amoebae in process of division; *C*, conjugation of two haploid amoebae; *kk*, the two uniting nuclei; *D*, binucleate plasmodium with a haploid amoeba enclosed in a digestive vacuole; *E*, plasmodium with six dividing nuclei (k_1) and with digestive vacuoles. (After JAHN.)

Very large plasmodia, often over a foot in breadth, of a bright yellow colour and creamy consistency, are formed by *Fuligo varians* (*Aethalium septicum*), and as the "flowers of tan" are often found in summer on moist tan bark. If exposed to desiccation, the plasmodia of this Myxomycete pass into a resting state, and become converted into spherical or strand-like SCLEROTIA, from which a plasmodium is again produced on a further supply of water. Finally, the whole plasmodium becomes transformed into a dry cushion- or cake-shaped fructification of a white, yellowish, or brown colour. The fructification, in this instance, is enveloped by an outer calcareous crust or rind, and is subdivided by numerous internal septa. It encloses numerous dark violet-coloured spores, and is traversed by a filamentous capillitium, in which are dispersed irregularly-shaped vesicles containing granules of calcium carbonate. A fructification of this nature, or so-called aethalium, consists, therefore, of a number of sporangia combined together, while in most of the Myxomycetes the sporangia are simple and formed singly.

The structure and nature of the sporangia afford the most convenient means of distinguishing the different genera. The usually brown or yellow sporangia are spherical, oval, or cylindrical, stalked (Figs. 311, 312 *D*) or not stalked (Fig. 312 *A*). They usually open by the rupture of the upper portion of the sporangium walls, the lower portion persisting as a cup (Figs. 311 *B*, 312 *A*). In *Cribraria* (Fig. 311 *C*) the upper part of the wall of the sporangium, which contains no capillitium, becomes perforated in a sieve-like manner. In *Stemonitis* (Fig. 311 *A*) the whole peridium falls to pieces, and the capillitium is attached to a columella, which forms a continuation of the stalk.

The order **Plasmodiophoraceae** [15] contains a few parasitic organisms, the chief of which is *Plasmodiophora Brassicae*, which causes tuberous swellings on the lateral roots of various species of *Brassica*. Its myxamoebae occur in numbers in the cells of the hypertrophied parenchyma of these swellings; after the contents of the host-cell have been exhausted they fuse into plasmodia, and these, after repeated nuclear divisions, give rise to the numerous spores, which are set free by the disorganisation of the plant. In the plasmodium a reduction division takes place, the resulting nuclei being those of the spores. The spores germinate like those of *Chondrioderma*, and the myxamoebae penetrate the roots of a young Cabbage-plant. The formation of true sporangia, however, does not take place, and this Slime Fungus represents a more simply organised or, in consequence of its parasitic mode of life, a reduced Myxomycete.

The systematic position of this order is still doubtful since it presents some cytological resemblances to the Chytridiaceae, which are placed with the Phycomycetes.

The small order of the **Acrasieae** occupies a lower position among the Myxomycetes. There are no swarm-spores. Amoebae arising from the spores increase in number by division and then become associated together, without fusion, to form an aggregate plasmodium. In the simplest cases this changes directly into a mass of spores. In some genera (*Dictyostelium*), however, a stalk is formed from some of the amoebae which remain sterile and are converted into firm cells; up this stalk other amoebae creep and form the mass of spores.

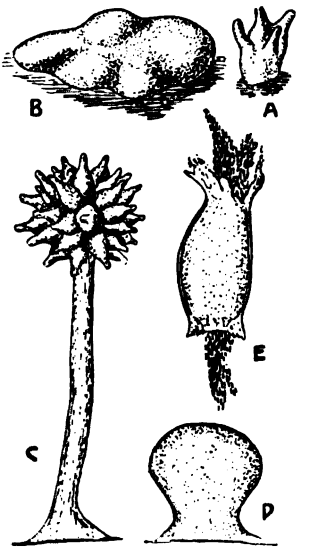


FIG. 315.—*A*, *Myxococcus digitatus*, bright red fructification occurring on dung (× 120). *B*, *Polyangium primigenium*, red fructification on dog's dung (× 40). *C*, *Chondromyces apiculatus*, orange fructification on antelope's dung. *D*, Young fructification (× 45). *E*, Single cyst germinating (× 200). (*A*, *B* after QUEHL; *C-E* after THAXTER.)

With some reservation the **Myxobacteriaceae** [16] may be placed here. Our accurate knowledge of them is in the first instance due to THAXTER, who grouped them with the Bacteria, but according to VAHLE they come nearer to the Myxomycetes. They are widely distributed and live saprophytically on the dung of animals, and in habit resemble the Myxomycetes. In the vegetative stage they appear as swarms of rod-shaped small cells connected together by the gelatinous substance secreted by the cells, and exhibit slow creeping movements. Ultimately they form fructifications that are usually brightly coloured; these have the form either of definitely limited masses of spores or of cysts which contain within a firm membrane the numerous spores arising by a transformation of the rod-shaped cells. The cysts are unstalked, or are raised singly or in groups on a stalk, formed, like the wall of the cyst, of gelatinous material derived from the rod-shaped cells excluded from spore formation. In germination the swarms of rod-shaped cells emerge from the ruptured cysts (Fig. 315).

Class V

Dinoflagellatae (1, 11, 17-19)

The Peridineae or Dinoflagellatae are connected as an independent and further developed group with certain Flagellata. They occur as unicellular, free-swimming organisms in fresh water, but for the most part in the sea, where, together with the Diatomeae, they constitute an important constituent of the phyto-plankton. Their cells are characterised by the possession of two long cilia or flagella which spring from the middle of the ventral surface in a longitudinal furrow; one of the cilia is directed backwards, the other is thrown into curves and lies in a transverse furrow (Fig. 316). The protoplast contains a nucleus, vacuoles of different sorts, and numerous brownish-yellow chromatophores; the latter contain a mixture of several pigments. Starch or oil is formed as the product of assimilation. While the Gymnodiniaceae (Fig. 317 *d*) have either naked cells or cells limited by a uniformly thickened cellulose wall, the typical Peridiniaceae have a wall composed of cellulose formed of polygonal plates; these are usually delicately sculptured and perforated with pores. The transverse furrow is formed by one girdle-shaped plate (Fig. 316).

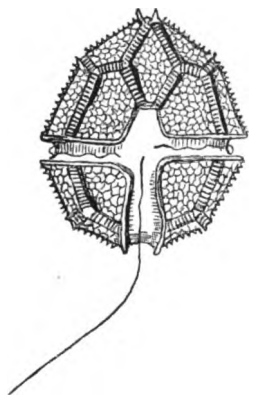


Fig. 316.—*Peridinium tabulatum.* (After Schilling.)

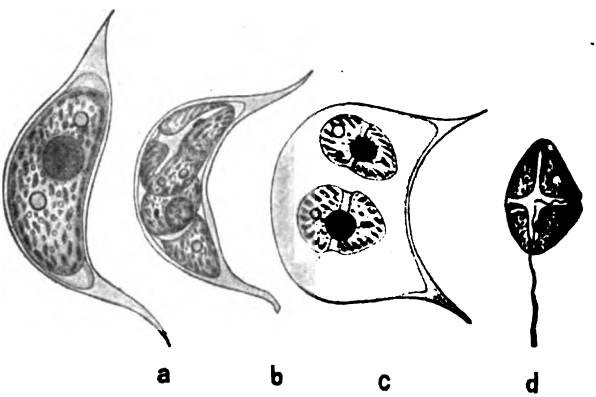


Fig. 317.—*Cystodinium Steinii*: *a*, cyst; *b*, division into two swarm cells; *c*, a cyst swelling; *d*, liberated swarm cell. (× 480. After Klebs.)

In many Peridineae of the plankton the plates bear special wing-like expansions

(Fig. 318) or the cells have long horn-like processes. These adaptations enable the organisms to remain floating in the water [18].

In some Dinoflagellatae the chromatophores are only represented by colourless leucoplasts. Such species live either as saprophytes or in the same way as animals. *Spirodinium hyalinum* is a colourless, naked, fresh-water form, the protoplast of which for the purpose of absorbing nourishment loses its cilia and assumes the form of an amoeba; in this condition it encloses and digests small Algae.

Some marine Peridineae (*e.g. Ceratium tripos, Peridinium divergens*) are phosphorescent, and play a considerable part in the phosphorescence of the sea [5].

Reproduction is effected by division usually of the motile cells. In certain genera (*Peridinium, Cystodinium* [Fig. 317]) the motile cells enter into a longer

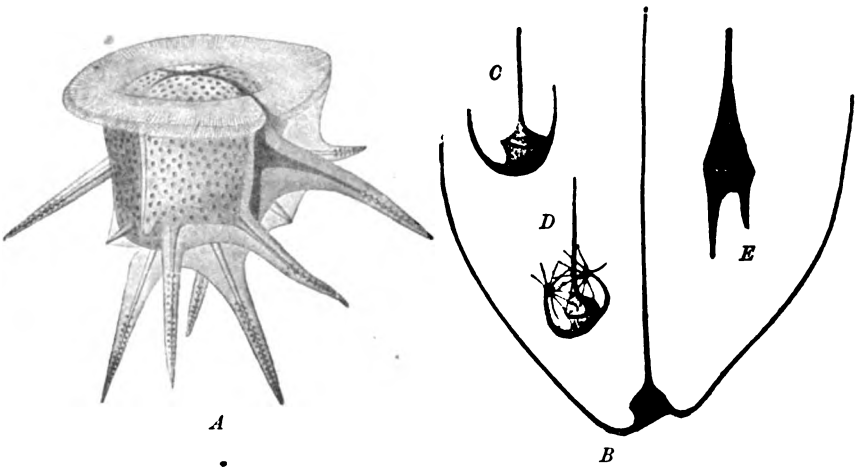


FIG. 318.—Peridineae of the plankton. *A, Ceratocorys horrida* var. *africana*, Indian Ocean (× 250); *B, Ceratium tripos intermedium* var. *aequatorialis*, Indian Ocean (× 62); *C, Ceratium tripos gibberum*, and *D, Ceratium palmatum*, Atlantic Ocean (× 62); *E, Ceratium furca*, Atlantic Ocean (× 125). (After G. KARSTEN.)

or shorter resting stage and form non-ciliated cysts in which division takes place; the daughter cells emerge from the swollen cysts as swarm cells. Lastly the motile stage may be completely suppressed and the two naked daughter cells emerge from the swollen cyst as non-ciliated cells provided with their own cell walls (*Hypnodinium*).

Some genera (*Ceratium*) form thick-walled resting-cysts within the old parent membrane.

Sexual reproduction has not been demonstrated in the Dinoflagellatae [19].

CLASS VI

Diatomeae (Diatoms) [1, 11, 20-23]

The Diatomeae (Bacillariaceae) constitute a very large class of unicellular Algae. They occur, usually associated together in large numbers, in both fresh and salt water, and also on damp soil.

The cells are either solitary or form colonies; they are free-floating, or are attached by means of gelatinous stalks, excreted by the cells themselves (Fig. 319). Sometimes the cells remain connected and form bands or zigzag chains, or, on the other hand, they are attached and enclosed in gelatinous tubes, while in the case of the marine genus *Schizonema* they lie embedded in large numbers in a gelatinous branching thallus. The cells also display a great diversity of shape; while generally bilaterally symmetrical, they may be circular or elliptical, rod- or wedge-shaped, curved or straight. The structure of their cell walls composed of pectic substance that is silicified is especially characteristic; it is formed of two halves or VALVES, one of which overlaps the other like

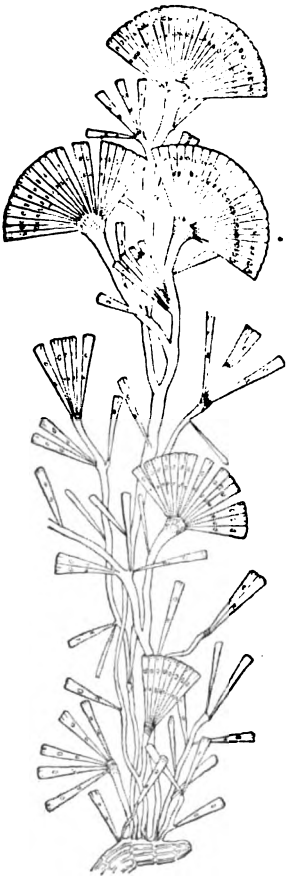


FIG. 319.—*Licmophora flabellata.* Colony of Diatoms with branched gelatinous stalks. (After SMITH, from GOEBEL'S *Organographie.*)

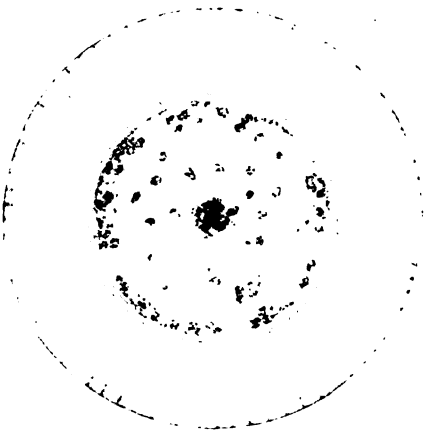


FIG. 320.—*Planktoniella sol.* Atlantic Ocean. A disc-shaped plankton diatom with a hollow floating wing arising from the girdle side. The protoplast contains a nucleus and numerous chromatophores. (× 322. After G. KARSTEN.)

the lid of a box. The cells thus present two altogether different views, according to the position in which they are observed, whether from the GIRDLE or VALVE SIDE (Fig. 79).

The lateral walls of the two valves are formed of the girdle pieces attached beneath the margins. In some genera the girdle side is extended by the introduction of annular or scale-shaped intermediate bands.

The two valves are so strongly impregnated with silica, that, even when subjected to intense heat, they remain as a siliceous skeleton, retaining the original form and markings of the cell walls. The walls of the cells, particularly on the valve side, are often ornamented with numerous fine, transverse markings or ribs, and also with small protuberances and pits. They are often perforated by open pores which serve to give exit to the gelatinous secretion.

The cell has always a central nucleus (Fig. 79) and one or two to four (Fig. 323) large, or numerous smaller chromatophores (Fig. 320) embedded in its parietal protoplasm. These chromatophores are flat, frequently lobed, and of a brownish-yellow colour. Pyrenoids are often present. The pigments are chlorophyll and yellow phycoxanthin. Globules of a fatty oil are also included in the cell contents, and take the place of starch as an assimilation product.

The Diatomeae multiply vegetatively by longitudinal division which always takes place in one direction. In this process the two valves are first pushed apart from one another by the increasing protoplasmic contents of the mother cell, which then divides longitudinally in such a direction that each of the two new cells retains one valve of the mother cell. After the division of the protoplasm of the mother cell is accomplished, each daughter cell forms, on its naked side, a new valve fitting into the old one. The two valves of a cell are therefore of different ages. In consequence of this peculiar manner of division, since the walls of the cells are silicified and incapable of distension, the daughter cells become successively smaller and smaller, until finally, after becoming reduced to a definite minimum size, they undergo transformation into AUXOSPORES. The auxospores are usually two or three times larger than the cells from which they arise, and by their further development they re-establish the original size of the cells.

The sexual reproduction consists of a conjugation of similar gametes.

The Diatoms include two orders, *Centricae* and *Pennatae*.

The auxospores in the Centricae, which are characterised by the centric structure of their valves, grow from vegetative cells without any previous process of conjugation. In the Pennatae, with a pinnate sculpturing of their valves, on the other hand, the auxospores develop from the zygotes resulting from a conjugation of gametes. The Pennatae have diploid vegetative cells, the reduction division taking place in the formation of the gametes. The Centricae are haploid and the simple chromosome-number has been attained at the division of the zygote, which so far as is known is in them the result of the fusion of ciliated gametes. The two groups of the Diatoms are thus sharply distinguished.

Order 1. Diatomeae Centricae

In these the valves are symmetrical about a centre, and have the sculpturing radially or concentrically arranged. The great majority of the forms of this order are marine, and play a large part in the composition of the plankton ([18]). The plankton diatoms are provided with special arrangements for floating, *e.g.* horn-like projections or wings of the cell wall such as are seen in Figs. 320 and 321.

The auxospore formation in the Centricae does not take place by the conjugation of two gametes but by the protoplasmic body of a cell becoming free from the cell walls and increasing in size; the enlarged cell is first surrounded by a weakly

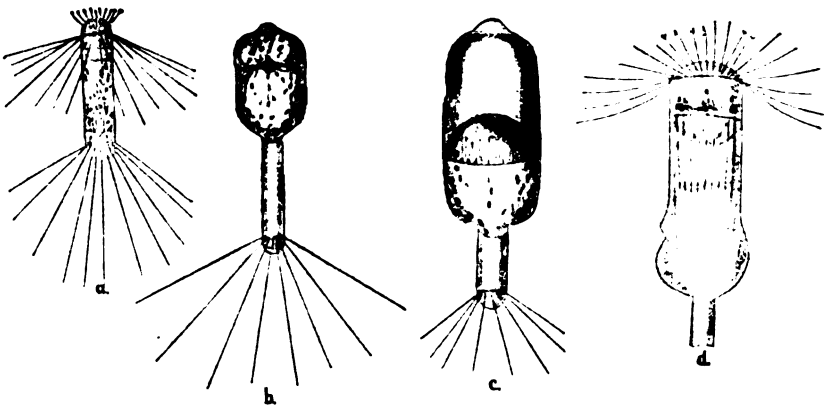


FIG. 321.—*Corethron Valdiviae*. From the Antarctic plankton. *a*, Cell with floating bristles and tentacles; *b*, Auxospore formation; the protoplast after casting off one valve has emerged from the other and, surrounded by the perizonium, has become four times its original size; *c*, the protoplast contracted within the perizonium and forming the new upper valve; *d*, the perizonium having disappeared above, the auxospore forms the new lower valve and escapes from the perizonium. (After KARSTEN.)

silicified membrane (perizonium), and in this the new valves are formed (Figs. 321, 322 *B*).

The Centricae further differ from the Pennatae by possessing a special method of

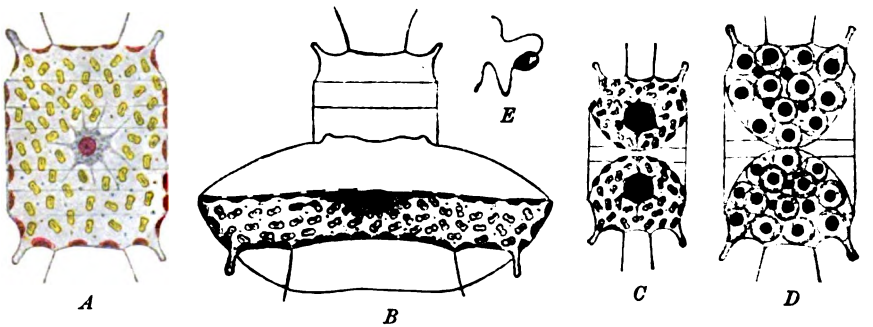


FIG. 322.—*Biddulphia mobiliensis*. *A*, View from the girdle side; *B*, auxospore formation; *C*, cell divided into two sporangia preparatory to the formation of microspores; *D*, spore formation in the sporangia; *E*, swimming microspore. (*A-D* × 228, *E* × 570. After P. BERGON.)

reproduction by means of so-called microspores (21); the formation of these has been accurately followed by BERGON in *Biddulphia mobiliensis*. A cell first divides into two daughter cells or sporangia, the contents of which round off and by repeated division form many (32) microspores. These emerge as naked swarm-spores, each

provided with two long cilia with knob-like thickenings at the tip (Fig. 322 *C-E*). These swarm-spores appear to behave as gametes, for KARSTEN observed in preserved material of *Corethron valdiviae* that the microspores conjugated in pairs to form zygotes. The zygote increased in size and divided into two cells. Each daughter cell had at first two nuclei, one of which later disappeared; it grew gradually into a mature individual of *Corethron*. The whole process may be compared with that described above in *Closterium* among the Desmidiaceae. The ciliated gametes or microspores which have been observed in other genera indicate a phylogenetic relation of the Diatomeae to the Flagellatae, especially to the Chrysomonadinae.

Order 2. Diatomeae Pennatae

In shape these are elongated, elliptical, or boat-shaped, but may be wedge-shaped; the valves have their sculpturing pinnate (Figs. 319, 323, 324). In many of the Pennatae (Fig. 79) a longitudinal line corresponding to an opening in the cell walls, and exhibiting swollen nodules at both extremities and in the middle, is distinguishable in the surface of the valves. Forms provided with such a median suture or RAPHE are characterised by peculiar creeping movements, resulting from the streaming protoplasm in the longitudinal slit of the raphe.

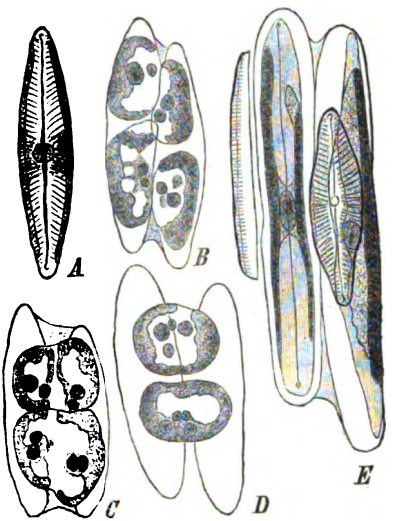


FIG. 323.—Formation of auxospores in *Navicula viridula*. *A*, Cell seen from the valve side. *B*, Two cells lying alongside one another; their contents have divided into two daughter cells, each of which possesses two nuclei. *C*, *D*, Conjugation in pairs of the daughter cells to form the auxospores, which at first contain four nuclei. *E*, The two full-grown auxospores. (× 500. After KARSTEN.)

The formation of the auxospores is accomplished in various ways. The process in *Navicula*, *Pleurosigma*, etc., may be taken as a starting point; two cells lay themselves side by side, and secrete a mucilaginous sheath. The nuclei of these cells undergo a reduction division, into four nuclei, two of which are large and two small. Each cell then divides into two gametes, each containing a large and small nucleus. The gametes escaping from the cell walls conjugate in pairs to form zygotes with four nuclei; the two large nuclei fuse, while the small nuclei disappear. Each zygote grows within a thin investment (perizonium) to form an auxospore several times the original size. This secretes two new valves and commences to divide vegetatively (Fig. 323).

In *Surirella* and *Cocconeis* (Fig. 324) the conjugating cells do not undergo division, but unite directly with one another. The nuclei, however, divide; in the former genus two nuclear divisions occur in each of the conjugating cells, resulting in one large and three small nuclei; in the latter genus there is only a single nuclear division giving one large and one small nucleus. The large nuclei fuse, the small ones degenerate.

In *Achnanthes subsessilis* the cell contents of a single cell divides into two daughter cells, which escape, and then fuse together to form the auxospore.

In some Pennatae the sexuality is lost and the auxospores arise apogamously. In *Synedra* the mother cell divides into two cells which grow into auxospores; the nuclei of the daughter cells undergo a division, but the resulting nuclei again fuse. In *Rhabdonema arcuatum* the process is similar, but the second nuclear division does not occur.

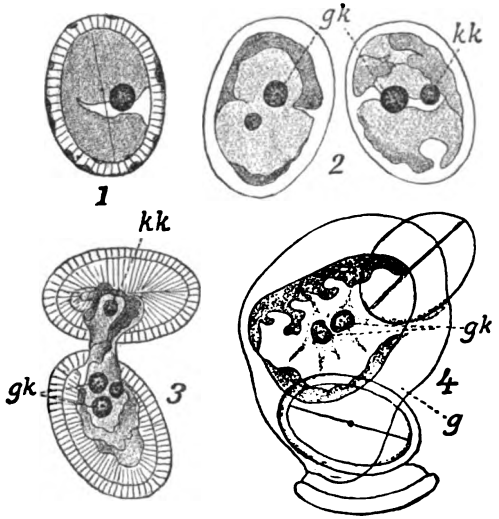


FIG. 324.—*Cocconeïs placentula*. *1*, Vegetative cell; *2*, pair of cells before conjugation; *3*, *4*, cells in process of conjugation. *gk*, Large nucleus; *kk*, small nucleus; *g*, gelatinous substance. (After KARSTEN, from OLTMANNS' *Algae*.)

Rhabdonema adriaticum goes a step farther; the nucleus divides, but one of the daughter nuclei is extruded from the protoplast. The undivided mother cell develops into the auxospore.

Many Pennatae occur in places where decomposing substances are present in abundance. Such species can assume a saprophytic mode of life, their chromatophores becoming colourless and reduced in size. It has been shown that some colourless species of *Nitzschia* which occur in the sea are exclusively dependent on organic substances for food, the reduction of their chromatophores and pigment being complete (22).

Navicula ostrearia is a Diatom occurring in the oyster-beds of the French coast, which serves as food for the oysters; its protoplasm contains a sky-blue pigment called marennin. This pigment is the cause of a green coloration of the oysters in which the marennin undergoes alteration and is accumulated (23).

Diatoms occur also as fossils. Their silicified valves form a large part of the deposits of SILICEOUS EARTH (Kieselguhr, mountain meal, etc.), and in this form they are utilised in the manufacture of dynamite.

On account of the extreme fineness of the markings of their valves, it is customary to employ certain species of Diatoms as test objects for trying the lenses of microscopes. *Pleurosigma angulatum* is commonly used for this purpose.

CLASS VII

Conjugatae (1, 11, 24-26)

This class of green fresh-water Algae includes unicellular and simply filamentous forms, and is clearly distinct from that of the Chlorophyceae. Their cells, which increase in number by cell division, are uninuclear, and differ from those of the Diatoms in having a cell wall which is not silicified, and in the presence of large green chloro-

plasts of complicated structure. Asexual reproduction by swarm-spores is wanting in them as in the Diatoms, with which they also show points of agreement in their sexual reproduction. This consists in the conjugation of two equivalent non-ciliated gametes to form a zygote or zygospore.

The Conjugatae and Diatomeae were formerly united in one group called the Zygophyceae, or on account of the non-ciliated gametes, the Acontae. This is no longer regarded as a natural grouping. It has been seen above that some Diatoms have ciliated gametes. The reduction division in the Conjugatae occurs after conjugation in the germinating zygote, while in the Pennatae it takes place at the formation of the gametes. The two groups have evidently originated independently from the Flagellatae.

1. The **Mesotaeniaceae**, the simplest of the unicellular Conjugatae, include only a few genera. They are distinguished from the following order by the cell wall of the shortly cylindrical cells not being formed of two halves. The mode of conjugation presents some differences. In *Cylindrocystis* (Fig. 325) the protoplasts of two cells fuse to form the zygote; the nuclei unite while the four chloroplasts persist. Before germination the zygote undergoes successive division into four cells, which then escape. Reduction is effected in the first nuclear division. In *Spirotaenia* the protoplasts of the conjugating cells first divide and the daughter cells unite in pairs to form the zygotes. Only two individuals arise from a zygote, the other two being suppressed.

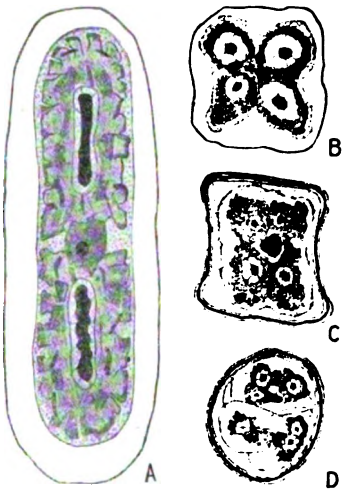


FIG. 325.—*A*, *Cylindrocystis Brebissonii*; the nucleus is in the centre between two large lobed chloroplasts with elongated pyrenoids. *B*, The zygote before, and *C*, after the fusion of the nuclei. *D*, The zygote before germination, with four daughter cells. (After KAUFFMANN.)

2. The **Desmidiaceae**, which occur in peaty pools, ponds, etc., are unicellular or their cells are united in rows; they are of great beauty and, like the Diatoms, exhibit a great variety of form. Their cells are composed of two symmetrical halves, separated, as a rule, from each other by a constriction. Each half contains a large, radiate chromatophore or a chromatophore composed of a number of plates. Within the chromatophores are disposed several pyrenoids, while the nucleus lies in the centre of the cell in the constriction. The cells themselves display a great diversity of form and external configuration, being sometimes rounded (*e.g. Cosmarium*, Fig. 326 *A*, *B*), sometimes stellate (*Micrasterias*, Fig. 326 *D*). The cell walls, which, as in the Diatoms, consist of separate halves, are frequently beset with wart- or horn-like protuberances and often provided with pores. In some genera there is no constriction between the two halves of the cell. This is the case, for instance, in the crescent-shaped *Closterium moniliferum* (Fig. 327 *F*), whose two chromatophores are elongated conical ribbed bodies, while in each end of the cell there is a small vacuole containing minute crystals of gypsum

in constant motion (25). Many Desmids are characterised by heliotactic movements; they protrude fine mucilaginous threads through the cell walls at their ends; by means of these they can push themselves along, and take up a position in a line with the direction of the incident rays of light.

Multiplication is effected by cell division. This is accomplished by the formation of a partition wall across the middle of the cell after the nuclear division is completed. Each daughter cell eventually attains the size and form of the mother cell, by the outgrowth of a new half on the side towards the plane of division (Fig. 326 *A*).

In conjugation two cells approach each other, and surround themselves with a

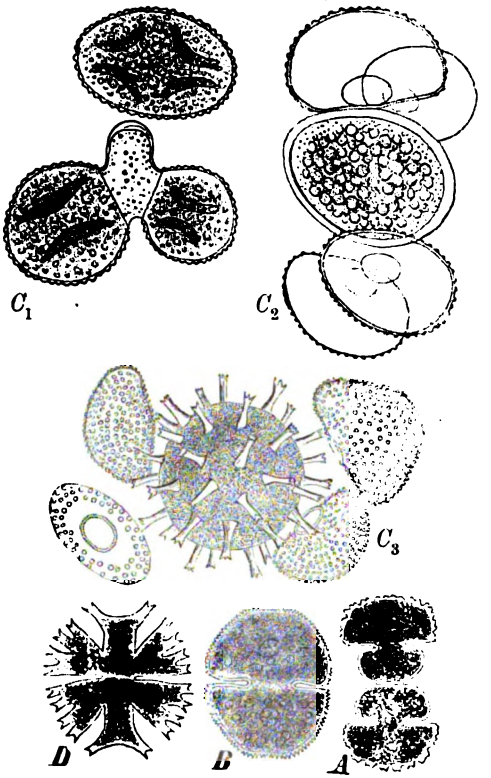


FIG. 326.—*A*, *Cosmarium coelatum*, dividing. *B*, *C*, *Cosmarium botrytis*. C_1, Two cells at right angles preparing for conjugation—the lower cell shows the conjugation canal; C_2, gametes fused into the young zygote; C_3, mature zygote; *D*, *Micrasterias crux melitensis*. (After RALFS; C_2, C_3 after DE BARY.)

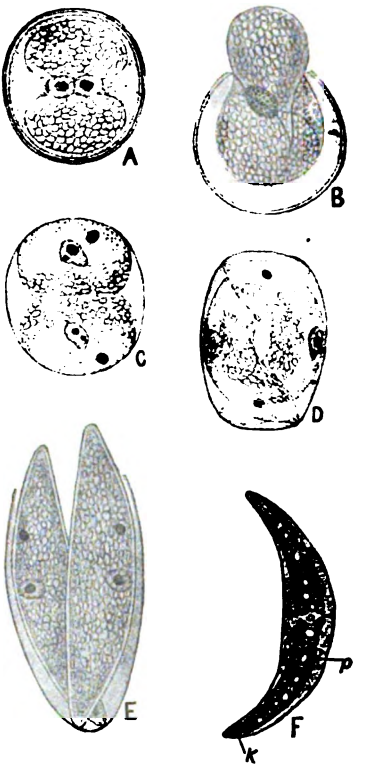


FIG. 327.—*Closterium*. *A*, Zygote before germination showing the two nuclei not yet united; *B*, germinating zygote with the nuclei united; *C*, division into two cells each containing one larger and one smaller nucleus; *D*, further state of germination; *E*, young plants escaping from the cell-membrane; *F*, *Closterium moniliferum*, mature plant. (*A*-*E* after KLEBAHN.)

mucilaginous envelope. Their cell walls rupture at the constriction, and parting in half allow the protoplasts to escape; these then unite to form a zygospore. The zygospores frequently present a very characteristic appearance, as their walls are often beset with spines (Fig. 326 *C*). The four empty cell halves may be seen close to the spore. In some Desmidiaceae the conjugating cells undergo a preliminary division, the daughter cells uniting in pairs.

The two sexual nuclei in the zygote do not fuse until germination of the latter is about to commence. The resulting nucleus then undergoes division, presumably with reduction, into four nuclei, two large and two small. Only two cells are formed from the zygote, each of which has thus two nuclei of different sizes; the smaller nuclei disappear (Fig. 327). The production of two cells on germination thus appears to be derived from the division into four cells seen in *Cylindro-*

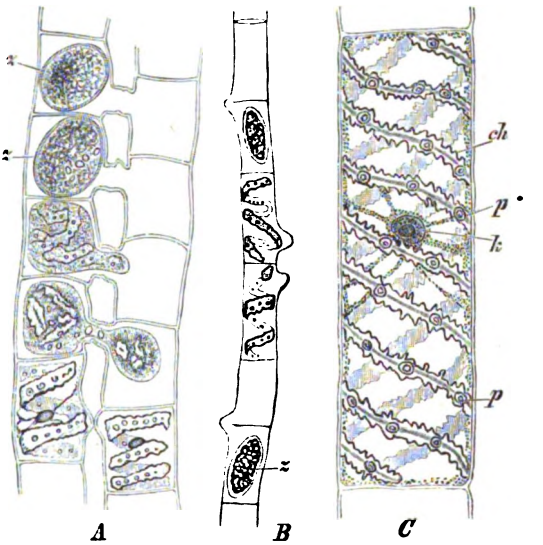


FIG. 328.—*A*, Conjugation of *Spirogyra quinina* (× 240). *B*, *Spirogyra longata* (× 150); *z*, zygospore. *C*, Cell of *Spirogyra jugalis*; *k*, nucleus; *ch*, chromatophores; *p*, pyrenoid (× 256).

cystis, and to stand to the latter as a reduced form. Two of the four chloroplasts in the zygote disappear, while the other two undergo a division before germination.

3. **Zygnemaceae.**—In this family, all of which are filamentous in character, the genus *Spirogyra*, with its numerous species, is the best known. It is commonly found in standing water, forming unattached masses of tangled green filaments. The filaments exhibit no distinction of base and apex, and are composed of simple rows of cells, which vary in length in different species. Growth results from the division and elongation of the cells in one direction only. Each cell has a large nucleus and one or several spiral green band-like chromatophores (Fig. 328 *C*). The cells of *Zygnema* contain two star-shaped chromatophores. The cells of the filament may separate under certain circumstances. The cell wall is smooth and without pores. The filaments can undergo movements.

CONJUGATION, in the case of *Spirogyra*, is preceded by the development of converging lateral processes from the cells of adjacent filaments. When two processes from opposite cells meet (Fig. 328 *A*) their walls become absorbed at the point of contact, and the whole protoplasmic contents of one cell, after contracting from the cell wall, passes through the canal which is thus formed into the opposite cell. The protoplasm and nuclei of the conjugating protoplasts then fuse together while the chloroplasts do not unite, but those of the entering protoplast disorganise. The resulting cell forms the zygospore invested with a thick wall, and filled with fatty substances and reddish-brown mucilage spheres. This form of conjugation, which is the one exhibited by most species, is described as scalariform (Fig. 328 *A*), as distinct from the lateral conjugation of some species, in which two adjacent cells of the same filament conjugate by the development of coalescing processes, which are formed near their transverse wall (Fig. 328 *B*). In some genera the zygote is formed midway in the conjugation tube.

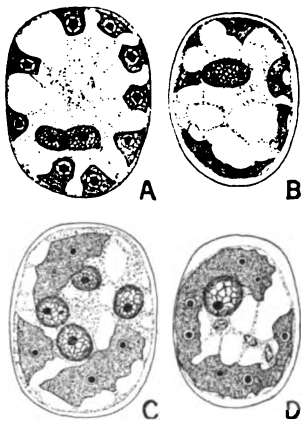


FIG. 329.—*Spirogyra longata*: zygotes of various age. *A*, The two sexual nuclei before fusion; *B*, after fusion; *C*, division of the nucleus of the zygote into four haploid nuclei; *D*, the three small nuclei degenerating. The chloroplasts are represented as cut across against the wall. (After TRÖNDLE.)

The conjugation nucleus of the young zygospore undergoes a tetrad division associated with the reduction in number of the chromosomes. One of the four nuclei becomes that of the young plant while the others appear as small nuclei, which then degenerate (Fig. 329). The chloroplasts of the gamete that passed across also degenerate. In this way one young plant arises which protrudes from the zygospore as a tubular growth and forms a filament by cell division ([26]).

CLASS VIII

Heterocontae ([1, 11, 27])

In the Heterocontae a number of genera of green Algae are included which were formerly placed in the Chlorophyceae but are now separated as an independent class derived from the Chrysomonadinae.

They are characterised by the yellowish green colour of the discoid chromatophores, which contain in addition to chlorophyll a yellow pigment which turns blue with acids, and form oil and not starch as the product of assimilation. The motile cells almost always have two cilia of unequal length attached rather to the side. The cell wall, which contains pectin and is usually silicified, in many cases consists of two overlapping halves. Some Heterocontae are unicellular, others form gelatinous colonies, while others are filamentous.

Reproduction is effected by swarm-spores, which in some genera are replaced by endogenous aplanospores. Resting cysts are also formed, and these, like the aplanospores, have a two-valved silicified membrane. In certain genera, in

addition to the swarm-spores, gametes which conjugate isogamously in pairs have been observed.

The Heterocontae form part of the Marine plankton in which a number of unicellular genera (*Meringosphaera*, *Halasphaera*) occur.

At the base of the class may be placed such Flagellate-like forms as *Chloramoeba heteromorpha* (Fig. 330), which lives in fresh water. The naked, amoeboid cell contains a nucleus and 2-6 yellowish-green chloroplasts; at the anterior end, just outside a vacuole, two cilia are situated which are of very unequal length. It is this last feature which gives the name to the group. *Chloramoeba* is one of those low green organisms which become colourless and lose the power of independent nutrition when cultivated in a nutritive solution in the dark. Thick-walled resting cells also occur.

Among the higher Hetero-

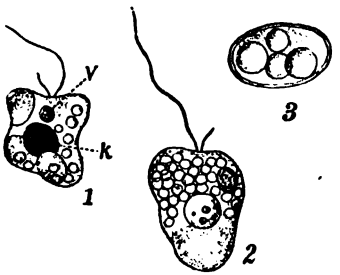


FIG. 330.—*Chloramoeba heteromorpha*: *1*, green form; *2*, colourless form; *v*, vacuole; *k*, nucleus. *3*, A resting cell. (After BOHLIN, from OLTMANNS' *Algae*.)

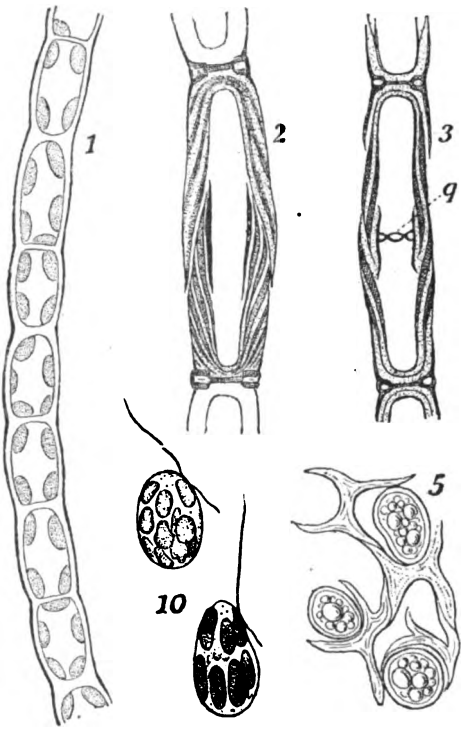


FIG. 331.—*Conferva bombycina*. *1*, Filament; *2*, *3*, formation of transverse wall (*q*) in cell division; *5*, formation of aplanospores by breaking down of the filament; *10*, Zoospores with cilia of unequal length. (After GAY (*1*, *5*), BOHLIN (*2*, *3*), LUTHER (*10*). From OLTMANNS' *Algae*.)

contae the genus *Conferva* (*Tribonema*), which is widely spread in fresh water, must be mentioned (Fig. 331). The plant consists of simple unbranched filaments the cells of which have peculiarly-constructed walls; the wall consists of two parts separated by an oblique annular split at the middle part of the cell. On cell division a new portion, H-shaped in longitudinal section, is intercalated. One or two zoospores are produced from a cell of the filament. In addition to zoospores thick-walled aplanospores arise by the separation by the cells of the filament.

The majority of the Heterocontae have uninucleate, only occasionally binucleate cells. But there are some genera with multinucleate cells in the class, *e.g.* *Ophiocytium* and *Sciadium*.

Class IX

Chlorophyceae ([1, 11, 26-38])

When the green Conjugatae and Heterocontae are separated there remains the large natural group of the Chlorophyceae, including several series of genera. The majority of these Algae live in fresh water or in damp situations; some large forms occur on the sea coast but do not contribute to the plankton. Their characteristic chloroplasts are of a pure green colour, frequently contain pyrenoids, and nearly always form starch. The asexual swarm-spores are pear-shaped, and in typical forms possess two or four cilia of equal length (on this account the group is sometimes termed Isocontae) and a curved or bowl-shaped chloroplast. In some genera the swarm-spores are replaced by non-motile aplanospores, and in certain of the more advanced genera (*Oedogonium*, *Vaucheria*) the swarm-spores are of more complicated structure, but can be derived from the typical simple form.

The swarm-spores exhibit phototactic movements by means of which they reach favourable conditions of illumination for their germination.

In all the orders sexual reproduction is usually effected by the conjugation of gametes which resemble the zoospores. In all the groups, except the Protococcales, isogamy is replaced by oogamy in the higher forms. The reduction division so far as is known takes place on the germination of the zygote.

Of the five orders included in the Chlorophyceae the Volvocales stand nearest to the Flagellata and, as is also the case with the Protococcales, include unicellular and colonial forms. The Ulotrichales and Siphonocladiales are filamentous; in the former the filaments are composed of uninucleate, in the latter of large multinucleate cells. The filaments are simple in the lower forms, but branched in the more advanced ones. The thallus of the Siphonales is formed of a single multinucleate cell.

Order 1. Volvocales

Typical representatives of this order are characterised by the cilia being retained by their cells in the vegetative stage; the plants are therefore motile. Each cell has a nucleus and a chloroplast. The Volvocales thus resemble the Flagellata.

Chlamydomonas (Fig. 333) and *Haematococcus* (Fig. 332) are widely distributed forms consisting of free-swimming cells ([29]). In the former the cell membrane is closely applied to the protoplast, at the anterior end of which two cilia and a red eye-spot are situated; in the latter genus the membrane is separated from the protoplast by a gelatinous layer except at the anterior end. *Haematococcus pluvialis* occurs commonly in puddles of rain-water, and, like *Chlamydomonas nivalis*, which gives rise to "red-snow" and occurs on snow in the Alps, etc., is characterised by the presence of a red pigment (haematochrome) in the cells.

Reproduction is both asexual, by swarm-spores, 2-8-16 of which are formed in a mother cell and are set free by rupture of the membrane, and sexual; the sexual reproduction is by conjugation of similar, small, biciliate gametes formed in large numbers (to 64) in a mother cell, and uniting in pairs by their anterior ends to form a zygote. In *Chlamydomonas coccifera*, according to GOROSCHANKIN [30], there is in contrast to the other species a marked differentiation in the sexual cells. Single cells become transformed into large, non-ciliated, female gametes or egg-cells; others divide and each gives rise to 16 small, biciliate male gametes. The transition to oogamy thus occurs in this group even among the isolated unicellular forms.

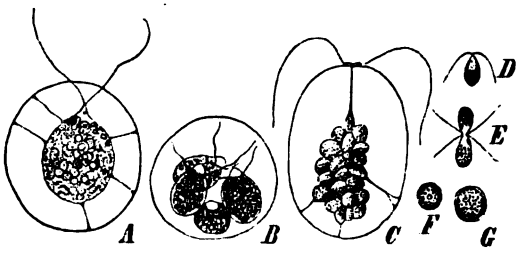


FIG. 332.—*A*, *B*, *Haematococcus pluvialis* (× 360): *A*, swarming cell; *B*, formation of swarm-spores. *C-G*, *Haematococcus Bütschlii*: *C*, formation of gametes (×400); *D*, gamete; *E*, conjugation of two gametes; *F*, *G*, zygotes (× 800). (*C-G* after BLOCHMANN.)

Polytoma uvella, which resembles *Chlamydomonas* in structure, is a colourless and saprophytic form (Fig. 333, 2).

Under certain conditions some Chlamydomonads lose their cilia and the cells enclosed in swollen gelatinous walls undergo divisions and form colonies. This is termed the Palmella stage. The cells can again become motile under favourable conditions.

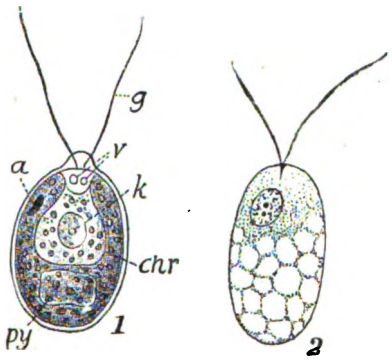


FIG. 333. — *1*, *Chlamydomonas angulosa* (after DILL); *g*, cilia; *v*, vacuole; *k*, nucleus; *chr*, chromatophores; *py*, pyrenoid; *a*, eye-spot. *2*, *Polytoma uvella* (after DANGEARD). (From OLTMANNS' *Algae*.)

The biciliate cells of *Pandorina*, *Eudorina*, *Volvox*, etc., are united in colonies or coenobia. In *Volvox* (Fig. 334), which may be regarded as the highest form in the order, the free-swimming colonies have the shape of a hollow sphere. The component protoplasts are connected by fine processes, so that the organism must be regarded as constituting a single individual. The sexual cells are differentiated into ova and spermatozoids. The egg-cells arise by the enlargement of single cells of the colony; they are large, green, non-motile cells surrounded by a mucilaginous wall. The small spermatozoids are elongated bodies of a bright yellow colour, provided with two cilia attached laterally below the colourless anterior end; they arise by the division of a cell of the colony into numerous daughter cells. After fusing with a spermatozoid within the cavity of the colony the egg-cell is transformed into the thick-walled, resting oospore. The vegetative reproduction of *Volvox* takes place by the division of single cells of the colony to form a new daughter colony; this corresponds to the formation of swarm-spores in other genera. *Eudorina* is also oogamous.

Order 2. Protococcales

These are unicellular green Algae, or their cells are united in colonies of various form; the vegetative cells have no cilia, and the cell or colony is consequently non-motile. Usually each cell contains a nucleus and only one chloroplast. Reproduction is by means of zoospores, in place of which in many genera non-

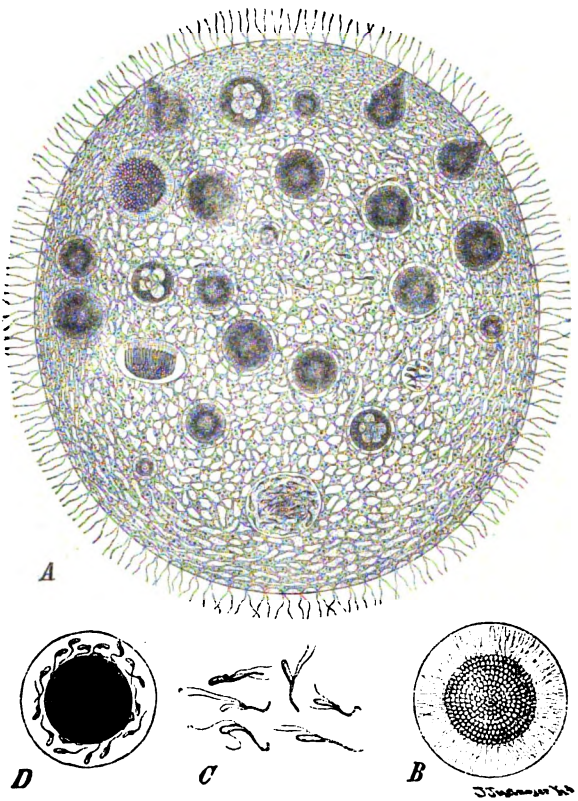


FIG. 334.—*Volvox globator*. *A*, Colony showing various stages of development of ova and spermatozoids (× 165). *B*, Bundle of spermatozoids formed by division from a single cell (× 530). *C*, Spermatozoids (× 530). *D*, Egg-cell surrounded by spermatozoids in the mucilaginous membrane (× 265). (After F. COHN.)

ciliated aplanospores are found. Sexual reproduction, when present, takes the form of conjugation of similar gametes. It has only been demonstrated in certain genera and appears not to have arisen in the simpler forms.

The simplest forms belong to the genera *Chlorococcum* and *Chlorella* ([31, 32]). The cells of the former are spherical, and occur in fresh water and also on damp substrata; they frequently take part in the composition of Lichen thalli. Asexual reproduction is by the production from a cell of a number of biciliate zoospores (Fig. 335); under certain conditions these are replaced by aplanospores without cilia. *Chlorella vulgaris* (Fig. 336) is a widespread Alga, the small cells of which

often live symbiotically in the protoplasts of lower animals (Infusoriae, *Hydra*, *Spongilla*, Planariae); it is multiplied only by division of the cells into 2, 4, or 8 aplanospores which surround themselves with walls and grow to the full size.

The simplest type of cell colony, consisting of four cells, is found in the genus *Scenedesmus*, which is widely spread in fresh water, and connects on to *Chlorella*. The commonest form, *Sc. acutus*, has spindle-shaped cells, while the colonies of *Sc. caudatus* are distinguished by four long horn-like prolongations of the cell wall (Fig. 337). In reproduction each cell divides in the direction of its length into four daughter cells, which on escaping from the parent cell form a new colony. More complicated cell colonies are met with in *Pediastrum* (Fig. 338), in which each cell-family forms a free-floating plate, composed internally of polygonal cells, while on the margin it consists of cells more or less acutely crenated. The formation of asexual swarm-spores is effected in *Pediastrum* by the division of the contents of a cell into a number (in the case of the species illustrated, *P. granulatum*, into 16) of naked swarm-spores, each with two cilia. The swarm-spores, on escaping through the ruptured cell wall (Fig. 338 *A*, *b*), are enclosed in a common envelope. After first moving vigorously about within this envelope, they eventually collect together and form a new cell-family. *Pediastrum* also possesses a sexual mode of reproduction. The gametes are all of equal size, and, except that they are smaller and are produced in greater numbers, are similar to the swarm-spores. They move freely about in the water, and in conjugating fuse in pairs to form zygotes. The further development of the zygotes into cell-families is not yet fully known.

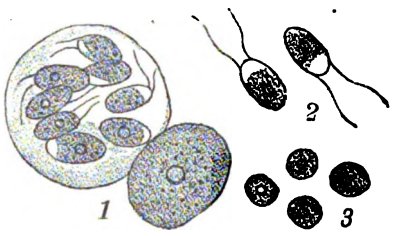


FIG. 335.—*Chlorococcum (Chlorosphaera) limicola*. *1*, Vegetative cell and cell divided into 8 zoospores; *2*, free zoospores; *3*, zoospores after they have formed cell walls. (After BEYERINCK, from OLTMANNS' *Algae*.)

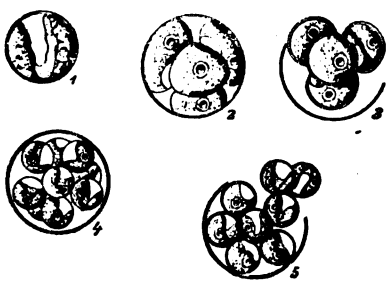


FIG. 336.—*Chlorella vulgaris*. *1*, Cell; *2*, *3*, division into four aplanospores; *4*, *5*, division into eight aplanospores. (After GRINTZESCO.)

The life-history of the Water-net (*Hydrodictyon utriculatum*) ([2, 33]) is essentially similar. It is one of the most beautiful of the free-floating, fresh-water Algae, the hollow cylindrical colonies being formed of elongated cells united together to form a many-meshed net.

The Protococcales like the Volvocales can be derived from the Flagellata. In contrast to the latter group the non-motile, non-ciliated condition of the cells has become prevalent as it has throughout the higher Algae. In some genera of the Protococcales even the spores do not develop cilia, although, as a rule, the reproductive cells of the Algae tend to retain the Flagellate character. The loss of motility is accompanied by a more complex external form of the cells.

Order 3. Ulotrichales

The Ulotrichales exhibit, as compared with the unicellular green Algae, an advance in the external segmentation of the thallus. It is always multicellular,

and, in most of the genera, consists of simple or branched filaments. The filaments are either attached by a colourless basal cell to the substratum (Fig. 340 *A*) or float free. The thallus of the marine genus *Ulva* (*Ulva lactuca*, SEA LETTUCE) has the form of a large, leaf-like cell surface, and is two layers of cells thick (Fig. 81, young plant). In *Enteromorpha* (Fig. 339) the thallus is ribbon-shaped, either cylindrical or flattened; when young it is two-layered, but later it becomes hollow, the wall thus consisting of one layer of cells. Although the majority of the Ulotrichales live in fresh or salt water, a few aerial forms (Chroolepideae) grow on stones, trunks of trees, and, in the tropics, on leaves. To this family belongs *Trentepohlia* (or *Chroolepus*) *Jolithus*, often found growing on stones in mountainous regions. The cell filaments of this species appear red on account of the haematochrome they contain and possess a violet-like odour.

The cells have always only one nucleus and also a single chloroplast.

The asexual reproduction is accomplished by the formation of ciliated swarm-spores. Sexual reproduction is effected either by the fusion of planogametes, or

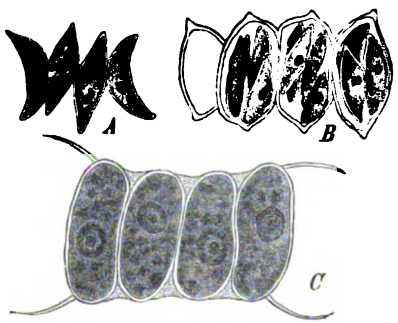


FIG. 337.—*A*, *Scenedesmus acutus*. *B*, The same, undergoing division. *C*, *Scenedesmus caudatus*. (× 1000. After SENN.)

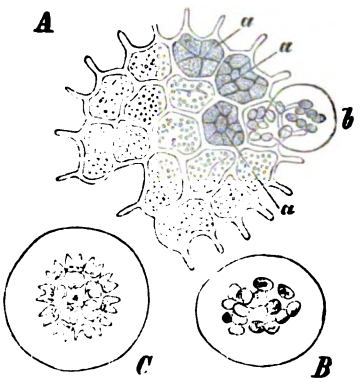


FIG. 338.—*Pediastrum granulatum*. *A*, An old cell-family: *a*, cells containing spores; *b*, spores in process of extrusion (the other cells have already discharged their spores). *B*, Cell-family shortly after extrusion of the spores. *C*, Cell-family 4½ hours later. (× 300. After AL. BRAUN.)

the sexual cells are differentiated as non-motile egg-cells and motile spermatozoids.

Ulothrix zonata (²) (Fig. 340 *A*) is one of the commonest filamentous Algae. The filaments of *Ulothrix* exhibit no pronounced apical growth; they are unbranched, attached by a rhizoid cell, and consist of rows of short cells; each cell contains a band-shaped chloroplast. The asexual reproduction is effected by means of swarm-spores, which have four cilia (*C*), and are formed singly or by division in any cell of the filament. The swarm-spores escape through a lateral opening (*B*) formed by absorption of the cell wall, and, after swarming, give rise to new filaments. The sexual swarm cells, or planogametes, are formed in a similar manner by the division of the cells, but in much greater numbers. They are also smaller, and have only two cilia (*E*). In other respects they resemble the swarm-spores, and possess a red eye-spot and one chromatophore. By the conjugation of the planogametes in pairs, zygotes (*F-H*) are produced, which, after drawing in their cilia, round themselves off and become invested with a cell wall. *Ulothrix* is dioecious, for gametes derived from the same filament do not fuse, but only those of distinct origin. After a shorter or longer period of rest the zygotes are

converted into unicellular germ plants (*J*), and give rise to several swarm-spores (*K*), which in turn grow out into new filaments. Under some conditions the planogametes can give rise to new plants parthenogenetically without conjugating. Further, the filaments can, in addition to the swarm-spores with four cilia described above, produce others of smaller size (micro-zoospores) which resemble the gametes. These possess four or two cilia, and as a rule die if the temperature of the medium is above 10°; below this temperature they come to rest after a few days and proceed to germinate slowly. This Alga is thus of interest from the incomplete sexual differentiation exhibited by its gametes.

The genera *Oedogonium* [34] and *Bulbochaete* may be quoted as examples of oogamous Ulotrichales. While the thallus of the latter is branched, the numerous species of *Oedogonium* consist of unbranched filaments, each cell of which possesses one nucleus and a single parietal chromatophore composed of numerous united bands. The asexual swarm-spores of Oedogonium are unusually large, and have a circlet of cilia around their colourless, anterior extremity (Fig. 341 *B*). In this case the swarm-spores are formed singly, from the whole contents of any cell of the filament (*A*), and escape by the rupture of the cell wall. After becoming attached by the colourless end they germinate, giving rise to a new filament. For the purpose of sexual reproduction, on the other hand, special cells become swollen and differentiated into barrel-shaped oogonia. A single large egg-cell with a colourless receptive spot is formed in each oogonium by the contraction of its protoplasm, while the wall of the oogonium becomes perforated by an opening at a point opposite the receptive spot of the egg. At the same time, other, generally shorter, cells of the same or another filament become converted into antheridia. Each antheridium usually gives rise to two spermatozoids. The spermatozoids are smaller than the asexual swarm-spores, but have a similar circlet of cilia. They penetrate the opening in the oogonium and fuse with the egg-cell, which then becomes transformed into a large firm-walled oospore. On the germination of the oospore its contents become divided into four swarm-spores, each of which gives rise to a new cell filament. In the adjoining figure (Fig. 342) a germinating oospore of *Bulbochaete* with four swarm-spores is represented.

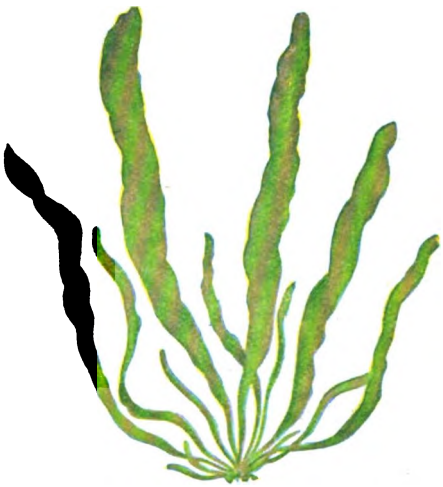


FIG. 339.—*Enteromorpha compressa*. (½ nat. size.)

In some species of *Oedogonium* the process of sexual reproduction is more complicated, and the spermatozoids are produced in so-called DWARF MALES. These are short filaments (Fig. 341 *C*, *a*) consisting of but few cells, and are developed from asexual swarm-spores (ANDROSPORES) which, after swarming, attach themselves to the female filaments, or even to the oogonia. In the upper cells of the

dwarf male filaments thus derived from the androspores, spermatozoids are produced which are set free by the opening of a cap-like lid (Fig. 341 *D*, *a*).

The genus *Coleochaete* [35] is also oogamous (Fig. 343). The long colourless neck of the flask-shaped oogonium opens at the tip to allow of the entrance of the spermatozoid. The spherical oospore increases in size and becomes surrounded by a single layer of pseudo-parenchymatous tissue derived from filaments that spring from the stalk cell of the oogonium and neighbouring cells. In this way a fruit-like body is formed. On germination the oospore undergoes a reduction division and divides into 16-32 wedge-shaped cells, then breaks up and liberates a swarm-spore from each cell.

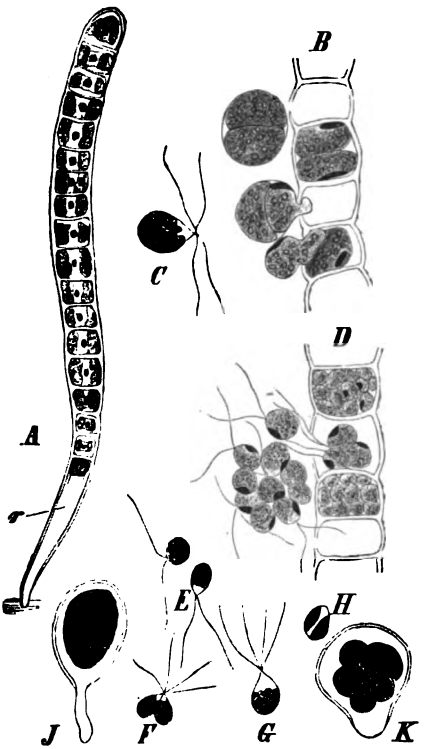


FIG. 340.—*Ulothrix zonata*. *A*, Young filament with rhizoid cell *r* (× 300); *B*, portion of filament with escaping swarm-spores; *C*, single swarm-spore; *D*, formation and escape of gametes; *E*, gametes; *F*, *G*, conjugation of two gametes; *H*, zygote; *J*, zygote after period of rest; *K*, zygote after division into swarm-spores. (*B-K* × 482. After DODEL.)

Order 4. Siphonocladiales

The Algae of this order are filamentous and usually branched; they are distinguished from the Ulotrichales by their large multinucleate cells, the chloroplasts of which are either solitary, large, and reticulately-formed, or appear as numerous small discs.

The genus *Cladophora*, numerous species of which occur in the sea and in fresh water, is one of the most important representatives of the order. *Cl. glomerata* (Fig. 84) is one of the commonest Algae in streams, often attaining the length of a foot. It is attached by rhizoid-like cells, and consists of branched filaments with typical apical growth which some other representatives of the order do not show. The structure of the cells is represented in Figs. 7, 9, and 18. Branching takes place from the upper ends of the cells by the formation of a protrusion which is cut off as the first cell of the branch. Asexual reproduction is by means of biciliate zoospores (Fig. 344), which arise in numbers from the upper cells of the filaments, and escape from these sporangia by a lateral opening in the wall. The sexual reproduction is isogamous as in *Ulothrix*.

Only in the genus *Sphaeroplea* has the sexual reproduction become oogamous. *S. annulina* consists of simple filaments and occurs in fresh water.

Many forms occur in the sea (*e.g. Siphonocladus*), and some have a highly complicated thallus, which is always, however, formed of branched filaments; by calcareous incrustation some forms come to resemble coral. *Acetabularia mediter-*

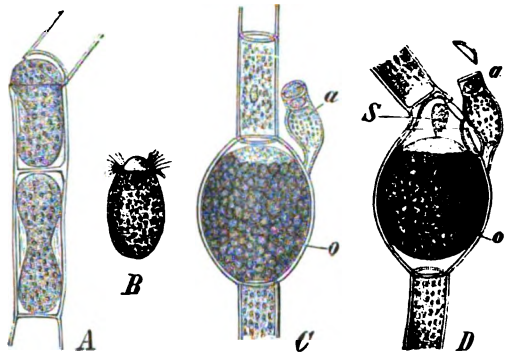


FIG. 341.—*A*, *B*, *Oedogonium*: *A*, escaping swarm-spores; *B*, free swarm-spore. *C*, *D*, *Oedogonium ciliatum*: *C*, before fertilisation; *D*, in process of fertilisation; *o*, oogonia; *a*, dwarf males; *S*, spermatozoid. (× 850. After PRINGSHEIM.)

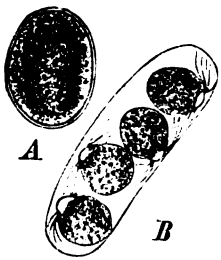


FIG. 342.—*Bulbochaete intermedia*. *A*, Oospore. *B*, Formation of four swarm-spores in the germinating oospore. (× 250. After PRINGSHEIM.)

ranea (Fig. 345) will serve as an example of such calcareous Algae. The thin stalk of the thallus is attached by means of rhizoids, while the umbrella-like disc consists of closely united tubular outgrowths, each of which is to be regarded as a gametangium. The contents of the latter do not form the biciliate gametes directly, but first divide into a large number of firm-walled cysts. These remain in the resting condition throughout the winter, and then give rise to numerous gametes which conjugate in pairs. The zygotes germinate promptly and grow into new plants.

Order 5. Siphonales

The Siphoneae are distinguished from the preceding groups of Algae by the structure of their thallus, which, although more or less profusely branched, is not at first divided by transverse septa. The cell wall thus encloses a continuous protoplasmic body in which numerous nuclei and small green chloroplasts are embedded. The same type of thallus is also met with in

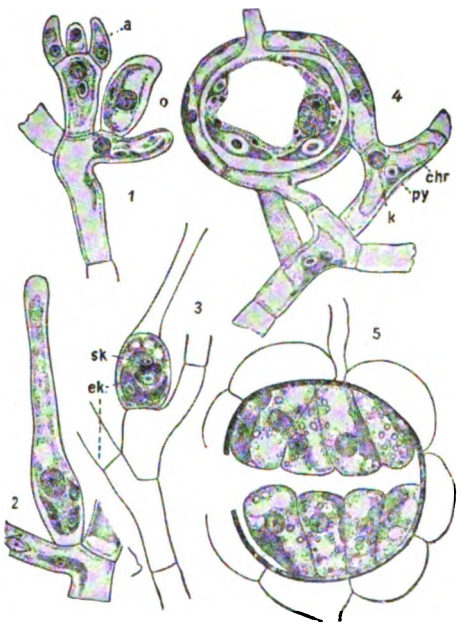


FIG. 343.—*Coleochaete pulvinata*. *1*, Antheridium (*a*) and young oogonium (*o*). *2*, Oogonium shortly before opening. *3*, Fertilised oogonium; *ek*, nucleus of the ovum; *sk*, male nucleus. *4*, Oospore enclosed to form the "fructification." *5*, Germinating oospore. (After OLTMANNS.)

the Phycomycetes or Algal Fungi.

The majority of the Siphoneae inhabit the sea, and on account of the complicated segmentation of their thallus, afford one of the most interesting types of algal development. The genus *Caulerpa* ([36]), represented by many species inhabiting the warmer water of the ocean, has a creeping main axis. Increasing in length by apical growth, the stem-like portion of the thallus gives off from its under surface profusely-branched colourless rhizoids, while, from its upper side, it produces green thalloid segments, which vary in shape in the different species. In *Caulerpa prolifera* (Fig. 346), which occurs in the Mediterranean, these outgrowths are leaf-like and are frequently proliferous. In other species they are pinnately lobed or branched. The whole thallus, however branched and segmented it may be, encloses but one cell-cavity, which is, however, often traversed by a network of cross-supports or trabeculae. Starch-forming leucoplasts are present in the colourless parts of the thallus.

The genus *Bryopsis*, on the other hand, has a delicate, pinnately-branched thallus ([37]). The thallus of *Halimeda*, the species of which occur in the warmer seas, is composed of

FIG. 344. — *Cladophora glomerata*. Swarm-spore. (× 500. After STRASBURGER.)

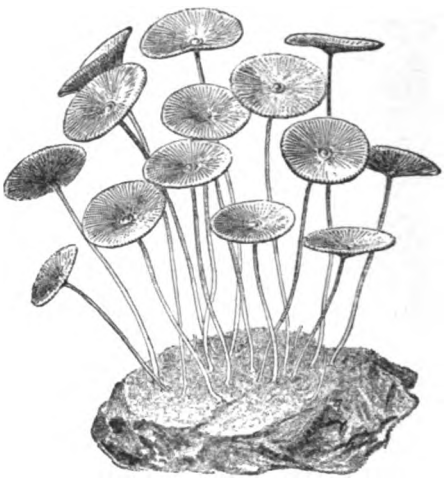


FIG. 345.—*Acetabularia mediterranea*. (Nat. size. After OLTMANNS.)

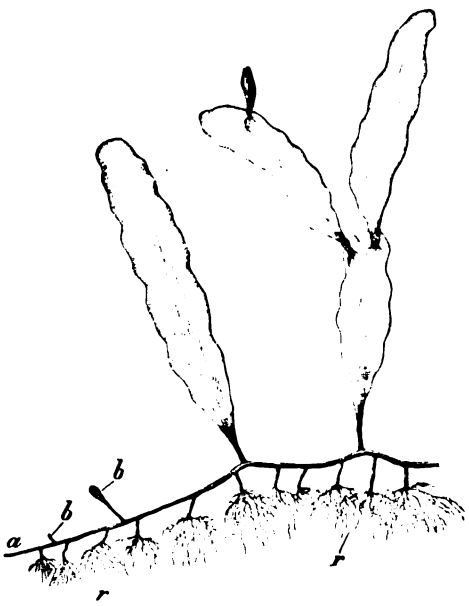


FIG. 346.—*Caulerpa prolifera*. The shaded lines on the thallus leaves indicate the currents of protoplasmic movement. *a*, Growing apex of the thallus axis; *b*, *b*, young thallus lobes; *r*, rhizoids. (¼ nat. size.)

flattened segments, and resembles an *Opuntia* on a small scale. By incrustation with lime it attains a hard, coral-like texture. The segments are formed of branched tubular filaments.

In *Bryopsis* the biciliate, pear-shaped, conjugating gametes are differentiated into a larger female cell with a green chromatophore and a smaller male cell, three times smaller than the female and with a single yellow chromatophore;

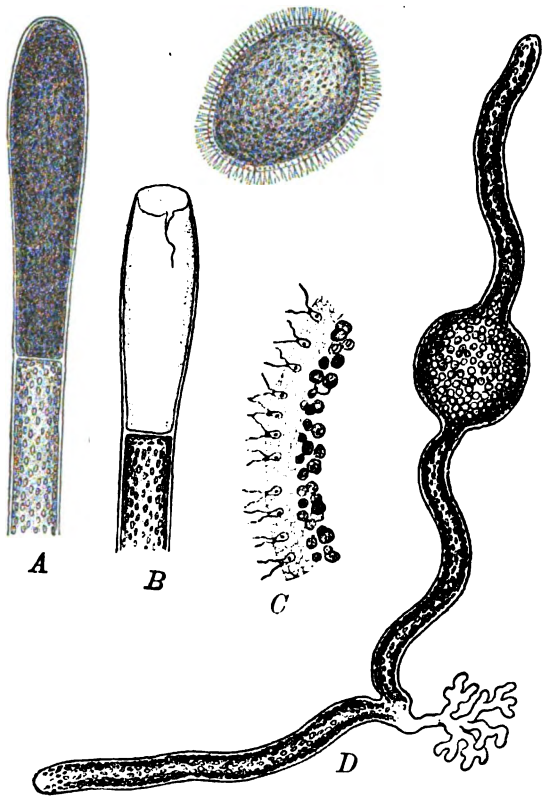


FIG. 347.—*Vaucheria sessilis*. *A*, Young sporangium. *B*, Zoospore with the sporangium from which it has escaped. *C*, A portion of the peripheral zone of a zoospore. *D*, A young plant with rhizoids developed from a zoospore. (*A*, *B* after GÖTZ; *D* after SACHS; from OLTMANNS' *Algae*. *C* after STRASBURGER.)

in *Vaucheria* and *Dichotomosiphon* oogamous reproduction is well marked (38). The latter Algae occur in fresh water or on damp soil. The thallus consists of a single branched filamentous cell attached to the substratum by means of colourless rhizoids (Fig. 347 *D*).

The swarm-spores of *Vaucheria*, which differ from those of the other Siphonales, are developed in special sporangia, cut off from the swollen extremities of lateral branches by means of transverse walls (Fig. 347). The whole contents of such a sporangium become converted into a single green swarm-spore. The wall

of the sporangium then ruptures at the apex, and the swarm-spore, rotating on its longitudinal axis, forces its way through the opening. The swarm-spore is so large as to be visible to the naked eye, and contains numerous nuclei embedded in a peripheral layer of colourless protoplasm. It is entirely surrounded with a fringe of cilia, which protrude in pairs, one pair opposite each nucleus. Morphologically the swarm-spores of *Vaucheria* correspond to the total mass of individual zoospores of an ordinary sporangium.

The sexual reproduction of *Vaucheria* is not effected, like that of the other Siphoneae, by the conjugation of motile gametes, from which, however, as the earlier form of reproduction, it may be considered to have been derived. The oogonia and antheridia first appear as small protuberances, which grow out into short lateral branches, and become separated by means of septa from the rest of the thallus (Fig. 348 *o*, *a*). At first, according to OLTMANNS and HEIDINGER, the rudiment of an oogonium contains numerous nuclei, of which all but one, the nucleus of the future egg-cell, retreat again into the main filament before the formation of the septum. In its mature condition the oogonium has on one side a beak-like projection containing only colourless protoplasm. The oogonium opens at this place, the oosphere rounding itself off. The antheridia, which are also multinucleate, are more or less coiled (*a*), and open at the tip to set free their mucilaginous contents, which break up into a number of swarming spermatozoids. The spermatozoids are very small, and have a single nucleus and two cilia inserted on one side. They collect around the receptive spot of the egg-cell, into which one spermatozoid finally penetrates. After the egg-cell has been fertilised by the fusion of its nucleus with that of the spermatozoid, it becomes invested with a wall and converted into a resting oospore. On germination the oospore grows into a filamentous thallus.

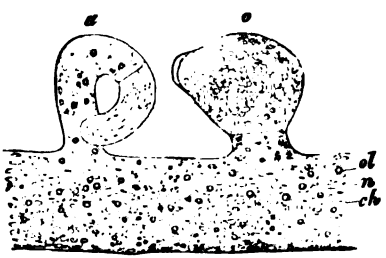


FIG. 348.—*Vaucheria sessilis*. Portion of a filament with an oogonium, *o*; antheridium, *a*; *ch*, chromatophores; *n*, cell nuclei; *ol*, oil globules. (× 240. After STRASBURGER.)

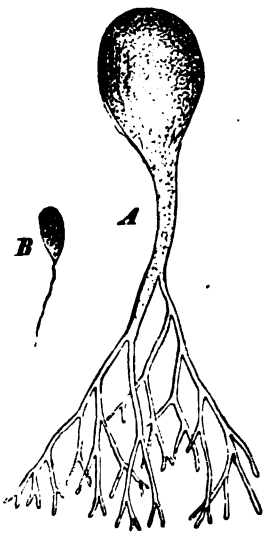


FIG. 349.—*Botrydium granulatum*. *A*, The whole plant. *B*, Swarm-spore. (*A* × 28; *B* × 540. After STRASBURGER.)

Botrydium granulatum (Fig. 349), which was formerly included in the Heterocontae, may be placed in the Siphoneae. This Alga is cosmopolitan and grows on damp clayey soil, where it forms groups of green balloon-shaped vesicles about 2 mm. in size. These are attached to the soil by branched colourless rhizoids. The whole plant corresponds to a single multinucleate cell; its protoplasm contains numerous green chloroplasts. The zoospores, produced in large numbers by the

division of the contents, escape by an opening at the summit. Each has a single cilium and contains two chloroplasts. After swarming the spore surrounds itself with a wall and grows into one of the balloon-shaped plants. Sexual reproduction is not known (2).

CLASS X

Phaeophyceae (Brown Algae) (1, 11, 39-47)

The Phaeophyceae, like the Chlorophyceae, can be derived from Flagellata. They attain a higher grade of organisation in their vegetative organs than do the Green Algae.

With the exception of a very few fresh-water species, the Phaeophyceae are only found in salt water. They attain their highest development in the colder waters of the ocean. They show great diversity in the form and structure of their vegetative body. The simplest representatives of this class (*e.g.* the genus *Ectocarpus*) have a filamentous thallus consisting of a branched or unbranched row of simple cells. Some Phaeophyceae, again, have a cylindrical, copiously-branched, multicellular thallus (*e.g. Cladostephus*), whose main axes are thickly beset with short multicellular branches (Fig. 89); while in other cases the multicellular thallus is ribbon-shaped and dichotomously branched (*e.g. Dictyota*, Fig. 83). Growth in length in both of these forms ensues from the division of a large apical cell (Figs. 89 and 90). Other species, again, are characterised by disc-shaped or globose thalli.

The Laminariaceae and Fucaceae include the most highly developed forms of the Phaeophyceae. To the first family belongs the genus *Laminaria* found in the seas of northern latitudes. The large stalked thallus of the Laminarias resembles an immense leaf; it is attached to the substratum by means of branched, root-like holdfasts, developed from the base of the stalk.

In *Laminaria digitata* and *L. Cloustoni* (Fig. 351), a zone at the base of the palmately-divided, leaf-like expansion of the thallus retains its meristematic character, and by its intercalary growth produces in autumn and winter a new lamina on the perennial stalk. The older lamina becomes pushed up and gradually dies, while a new one takes its place and becomes in turn palmately divided by longitudinal slits. The large size of their thalli is also characteristic of the Laminarias; *L. saccharina* (North Sea), for instance, has an undivided but annually renewed lamina, frequently 3 m. long, and a stalk more than 1 cm. thick.

The greatest dimensions attained by any of the Phaeophyceae are exhibited by certain of the Antarctic Laminariaceae. Of these, *Macrocystis pyrifera* (Fig. 350) is noted for its gigantic size; the thallus grows attached to the sea-bottom at a depth of 2-25 m., and, according to SKOTTSBERG (39), is at first dichotomously branched. Single shoots of the thallus grow to the surface of the water, and floating there attain a great length; they bear on one side long flat lobes divided at their free ends, and having at the base of each a large swimming bladder. In the Antarctic SKOTTSBERG measured examples 70 m. long, while FRYE, RIGG, and CRANDALL

determined the length on the coasts of California as 45·7 m. Other noteworthy forms are the Antarctic species of *Lessonia*, in which the main axis is as thick as a man's thigh; from it are given off lateral branches with hanging leaf-like segments. The plant attains a height of several metres, and has a tree-like habit of growth.

The Fucaceae [40], although relatively large, do not compare with the Laminariaceae in size. As examples of well-known forms of this order may be cited

FIG. 350.—*Macrocystis pyrifera*, Ag. *a*, Younger, *b*, older thallus. ($\frac{1}{10}$ nat. size. After SKOTTSBERG.)

Fucus vesiculosus, which has a ribbon-shaped, dichotomously-branching thallus with air-bladders, *Fucus platycarpus* without bladders, and *Fucus serratus* (Fig. 352) with a toothed thallus. They are fastened to the substratum by discoid holdfasts, and growing sometimes over 1 metre long are found covering extended areas of the littoral region of the sea-coast. *Sargassum*, a related genus chiefly inhabiting tropical oceans, surpasses the other Brown Seaweeds in the segmentation of its thallus. The thallus of *Sargassum* shows, in fact, a distinction into slender, branched, cylindrical axes with lateral outgrowths, which, according to their function, are differentiated as foliage, bracteal, or fertile segments, or as air-bladders.

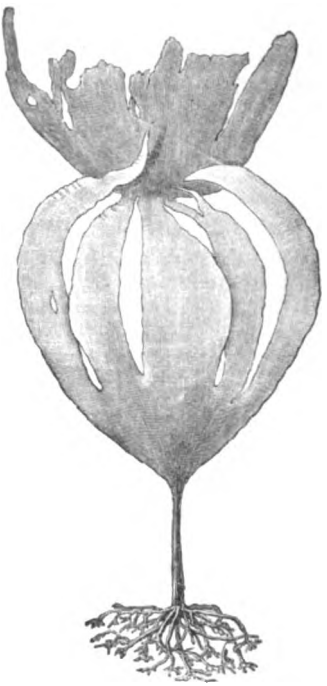


FIG. 351.—*Laminaria Cloustoni*, North Sea. (Reduced to $\frac{1}{4}$.)

The species of *Sargassum* which in the warmer regions of the ocean often form large yellowish-brown floating masses are worthy of note. In the Sargasso Sea of the Atlantic Ocean there are according to BÖRGESEN two species (*S. natans* = *S. bacciferum* and *S. fluitans*) which have this exclusively pelagic mode of life. They have reproduced here for ages by vegetative budding, though originally coming from attached species of the coasts of the West Indies and tropical America [41]. *S. natans* also occurs in the Pacific.

The cells of the Phaeophyceae [42] have usually but one nucleus. They contain a larger or smaller number of simple or lobed, disc-

shaped, brown chromatophores, giving to the algae a yellowish-brown or dark-brown colour. In addition to the pigments of chlorophyll

FIG. 352.—*Fucus serratus.* To the left the end of an older branch bearing conceptacles. (½ nat. size.)

they contain a special yellow pigment, phycoxanthin (fucoxanthin). A polysaccharid called laminarin arises as a metabolic product from glucose, while in addition mannite is formed. Small vacuoles containing a tannin-like substance called fucosan are generally distributed in the

cells; this is a by-product of the process of assimilation. Among the more highly developed forms the thallus exhibits a well-differentiated anatomical structure. The outer cell layers, as a rule, function as an assimilatory tissue, the inner cells as storage reservoirs. In the Laminariaceae and Fucaceae structures closely resembling the sieve-tubes of the cormophytes occur, and conduct albuminous substances.

Even in the largest Sea-weeds (including the Red Algae) intercellular spaces containing air are wanting in the tissues. According to KNIEP the gaseous interchanges in assimilation, and especially in respiration, are on this account difficult in the more massive Algae. On the other hand, gases readily diffuse through algal cell walls.

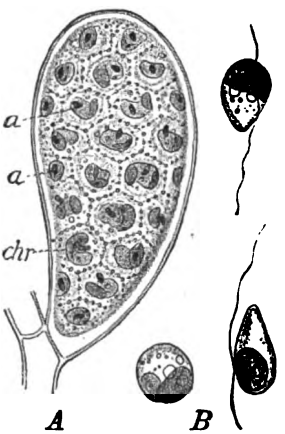


FIG. 353.—*A*, *Pleurocladia lacustris*. Unilocular sporangium with its contents divided up into the zoospores; *a*, eye-spot; *chr*, chromatophore. (After KLEBAHN.) *B*, *Chorda filum*. Zoospores. (After REINKE.) (From OLTMANNS' *Algae*.)

Four orders of the Phaeophyceae may be distinguished. The *Phaeosporeae* include forms with simple structure of the thallus which is frequently filamentous. They are vegetatively reproduced by means of zoospores and sexually by ciliated gametes. They thus resemble the simpler Green Algae. The *Tilopteridaceae* and *Dictyotaceae* stand at a higher level, their sexual cells being differentiated as large non-motile egg-cells and small ciliated spermatozoids. Their sexual cells are formed on special sexual individuals or gametophytes. From the fertilised egg the asexual generation or sporophyte is developed; this is similar to the gametophyte, but produces the asexual spores so that there is a well-marked alternation of generations which is also apparent in some of the Phaeosporeae. In the *Laminariaceae* also there is oogamy and a regular alternation of generations, but the sporophyte and gametophyte are very unlike, the latter being a small filamentous dwarf plant. The *Fucaceae* are also characteristically oogamous, but produce no spores and thus lack an alternation of generations.

The zoospores, gametes, and spermatozoids are spindle-shaped and always have a red eye-spot and two laterally inserted cilia, one directed forwards and the other backwards. They have a great resemblance to certain brownish-yellow Flagellata.

Order 1. Phaeosporeae

In this order are included the majority of the Phaeophyceae. A sexual multiplication is effected by means of swarm-spores, which are produced in large numbers in simple (unilocular) sporangia and germinate shortly after swarming (Fig. 353).

In addition to unilocular sporangia, multilocular sporangia are produced in the Phaeosporeae (Fig. 354). Each cell of the multilocular sporangium produces a single swarm-spore, rarely several. The conjugation of these swarm-spores has been observed in some genera. On this account these swarm-spores must be termed

planogametes, and the corresponding sporangia gametangia. The degree of sexual differentiation varies, and in some cases the swarm-spores produced in multilocular

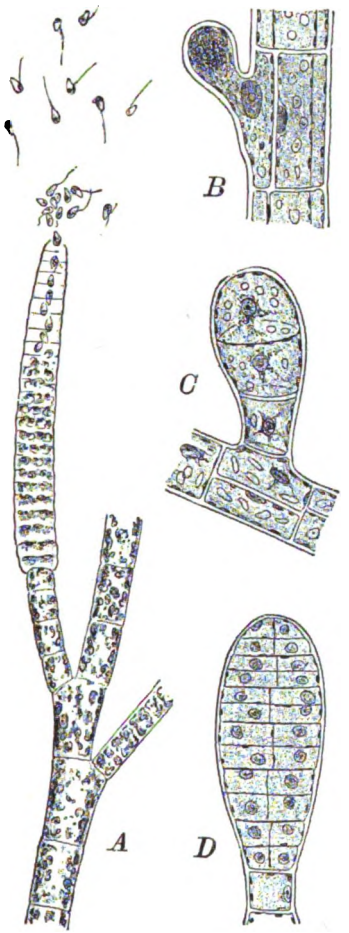


FIG. 354.—*A*, *Ectocarpus siliculosus*. Plurilocular sporangium liberating its contents. (After THURET.) *B*, *C*, *D*, *Sphacelaria cirrhosa*, development of the plurilocular sporangium. (After REINKE.) (From OLTMANNS' *Algæ*.)

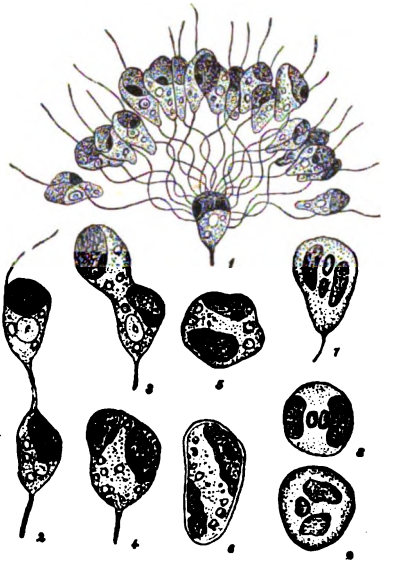


FIG. 355.—*Ectocarpus siliculosus*. *1*, Female gamete surrounded by a number of male gametes; seen from the side. *2-5*, Stages in the fusion of gametes. *6*, Zygote after 24 hours. *7-9*, Fusion of the nuclei in conjugation, as seen in fixed and stained material. (*1-5* after BERTHOLD; *6-9* after OLTMANNS.)

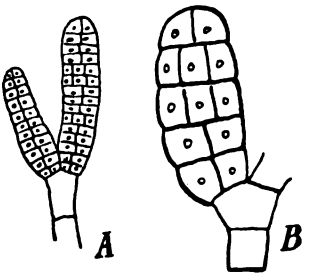


FIG. 356.—*A*, Antheridium; *B*, Oogonium of *Cutleria multifida*. (× 400. After REINKE.)

sporangia can germinate without conjugating, as was seen to occur in *Ulothrix* among the Chlorophyceae.

Ectocarpus siliculosus (Fig. 354) will serve as an example of the mode of conjugation of gametes produced from multilocular gametangia. The gametes are similar in form, but their different behaviour allows of their distinction into male and female which are formed in distinct gametangia, borne on the same or different

plants. The female gamete becomes attached to a substratum, and numerous male gametes gather around it (Fig. 355, 1). Ultimately a male gamete fuses with the female to form a zygote (Fig. 355, 2-9). This contains after the fusion a single nucleus, but two chromatophores, and soon becomes attached and surrounded by a cell wall; it grows into a new plant.

In other Phaeophyceae the distinction between the two kinds of gametes is expressed in their shape and size. The Cutleriaceae afford a particularly good transition from isogamy to oogamy and a differentiation of the gametangia into antheridia and oogonia (Fig. 356).

In certain Phaeosporeae, *e.g.* the Cutleriaceae ([43]), a regular alternation of generations is found. The haploid sexual plants alternate with diploid asexual individuals,

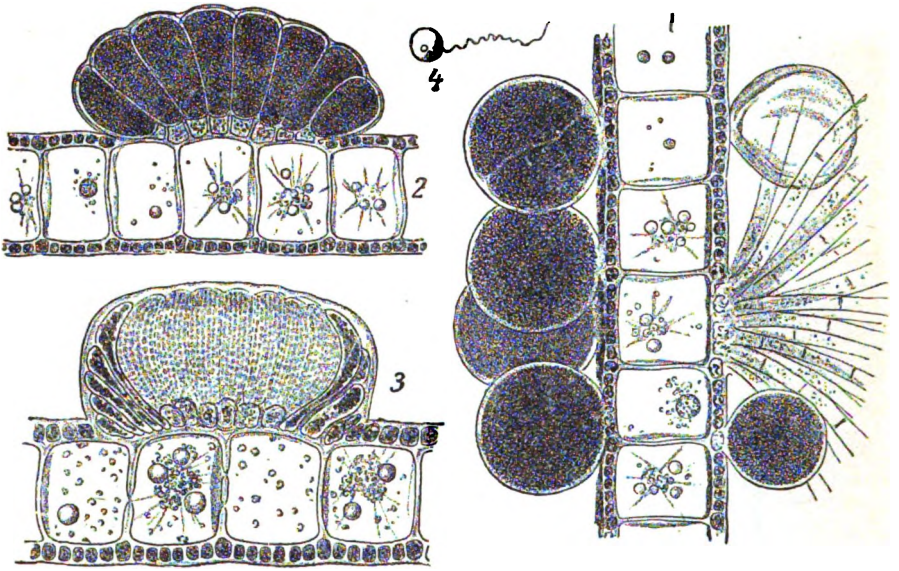


FIG. 357.—*Dictyota dichotoma*. Transverse sections of the thallus. *1*, With tetrasporangia; *2*, with a group of oogonia; *3*, with a group of antheridia (after THURET). *4*, Spermatozoid (after WILLIAMS). (From OLTMANNS' *Algae*.)

the reduction division taking place in the zoosporangia. In *Zanardinia* the two generations are alike and have a disc-shaped thallus. In *Cutleria*, on the other hand, they are unlike, the sexual plant having erect, dichotomously-divided shoots, while the sporophytic plants (*Aglaozonia*) form flat, lobed, prostrate discs. The alternation of generations is not always strictly maintained in *Cutleria*, since both sporophyte and gametophyte may give rise to its like.

Order 2. Tilopteridaceae ([44])

This order includes only a few forms which in vegetative habit correspond to the simpler Phaeosporeae such as *Ectocarpus*. A single large egg-cell is produced in each oogonium, while the antheridia give rise to small biciliate spermatozoids. In the asexual sporangia there is no division into spores, but the contents become a single large monospore with four nuclei and enclosed by a cell wall, while in the Dictyotaceae four free spores are formed.

Order 3. Dictyotaceae (45)

Only a small number of forms belong to this family. The fan-shaped *Padina pavonia*, which occurs in the Mediterranean, and *Dictyota dichotoma*, with a forked ribbon-shaped thallus, which is widely spread in the European seas (Fig. 83), are examples. The spores are formed as in the Red Algae in sporangia ; usually there are four spores (tetraspores), less commonly eight. They have no cell walls and are unprovided with cilia and must be termed aplanospores (Fig. 357, 1). The tetrasporangia may be derived from the unilocular sporangia of the Phaeosporeae. The oogonia and antheridia in *Dictyota* are grouped in sori (Fig. 357, 2, 3), and

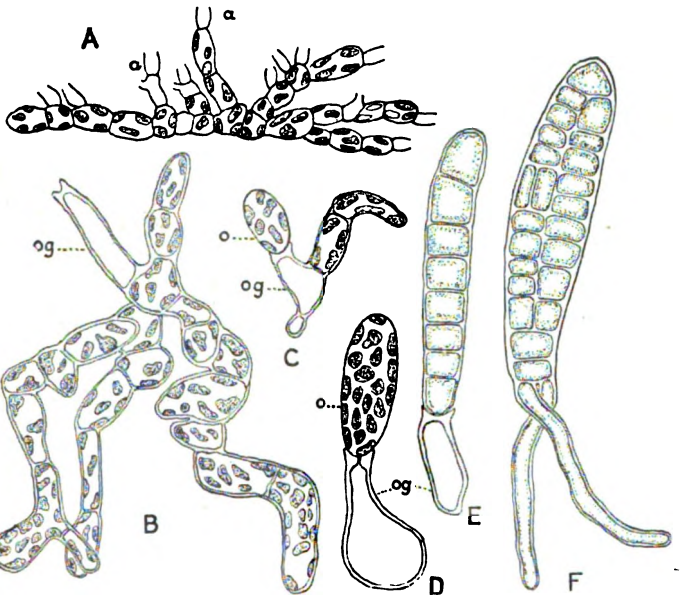


FIG. 358.—*Laminaria digitata*. *A*, Male gametophyte ; *a*, empty antheridia. *B*, *C*, *D*, Female gametophytes (*B* is large, *C* small, while *D* is reduced to a single oogonium); *og*, oogonium ; *o*, egg-cell. *E*, Young sporophyte, still seated on the empty oogonium. *F*, Further developed sporophyte with the rhizoids. (*A* × 600 ; *B* × 202 ; *C* × 322 ; *D* × 625 ; *E* × 322 ; *F* × 390. After H. KYLIN.)

arise from adjacent cortical cells, each of which divides into a stalk cell and the oogonium (or antheridium). The peripheral cells of the antheridial group remain sterile and form a kind of indusium. Each oogonium forms a single uninucleate oosphere ; the antheridia become septate, resembling the plurilocular gametangia, and each cell gives rise to a spermatozoid. This, in contrast to the spermatozoids of other Brown Algae, has a single long cilium, inserted laterally. The zygote germinates without undergoing a period of rest.

Dictyota is dioecious. The male and female plants arise from the asexually-produced tetraspores ; from the fertilised ovum plants which bear tetraspores are developed. In the tetrad division in the sporangia the number of chromosomes becomes reduced from 32 to 16, and the reduced number is maintained in all the nuclei of the sexual plants, the double number being again attained in fertilisation. There is thus a true alternation of generations. The sexual generation (gametophyte)

and the asexual generation (sporophyte) do not, however, show differences in structure.

Order 4. Laminariaceae (46)

The regular alternation of generations of these plants, which are the largest of the Brown Algae, corresponds with that in Ferns in that the gametophyte in contrast to the sporophyte is very small. The large sporophyte bears club-shaped or cylindrical sporangia forming an extensive superficial layer. Each surface cell of the thallus is prolonged as a club-shaped sterile cell or paraphysis beside which the sporangia arise as shorter cells. The reduction division takes place in the sporangia. From the biciliate swarm-spores minute filamentous male and female gametophytes develop (Fig. 358). The former are abundantly branched, while the latter consist of few cells and in extreme cases may be reduced to a single cell. The male gametophytes bear the antheridia beside or behind one another at the tips of the branches. Each antheridium gives rise to one spermatozoid. Any cell of the female gametophyte may form an oogonium, from an opening at the summit of which the naked egg-cell emerges. This remains in front of the opening and after fertilisation (which has not been observed) proceeds to grow into the young sporophyte (Fig. 358 *E*, *F*). The oogonia and antheridia are homologous with the gametangia of the Phaeosporeae.

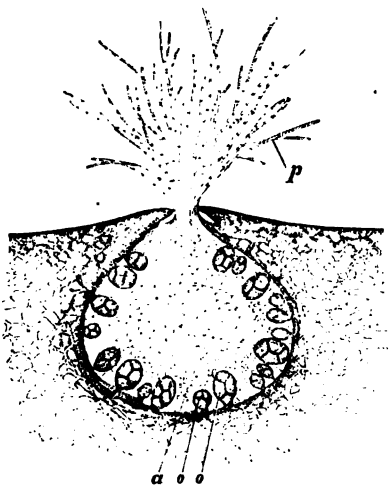


FIG. 359. — *Fucus platycarpus*. Monoecious conceptacle with oogonia of different ages (*o*), and clusters of antheridia (*a*); *p*, paraphyses. (× circa 25. After THURET.)

PASCHER has observed on cultivated young sporophytes of *Laminaria saccharina* an extremely early production of sporangia. Thus the sporophyte, which is usually of large size, may under particular external conditions undergo profound reduction in size. A point of view is thus attained from which the striking dimorphism of the two generations may be explained.

Order 5. Fucaceae (47)

Asexual reproduction is wanting in this order, while sexual reproduction is distinctly oogamous. The oogonia and antheridia of *Fucus* are formed in special flask-shaped depressions termed CONCEPTACLES, which are crowded together below the surface in the swollen tips of the dichotomously-branched thallus (cf. *F. serratus*, Fig. 352). The conceptacles of *F. platycarpus* (Fig. 359) contain both oogonia and antheridia, while *F. vesiculosus*, on the contrary, is dioecious. From the inner wall of the conceptacles, between the oogonia and antheridia, spring numerous unbranched sterile hairs or PARAPHYSES, some of which protrude in tufts from the mouth of the conceptacle (Fig. 359 *p*). The antheridia are oval in shape, and are formed in clusters on special short and much-branched filaments (Figs. 359 *a*, 360, 1). The contents of each antheridium separate into sixty-four spermatozoids, which are dis-

charged in a mass, still enclosed within the inner layer of the antheridial wall (Fig. 360, 2). Eventually set free from this outer covering, the spermatozoids appear as

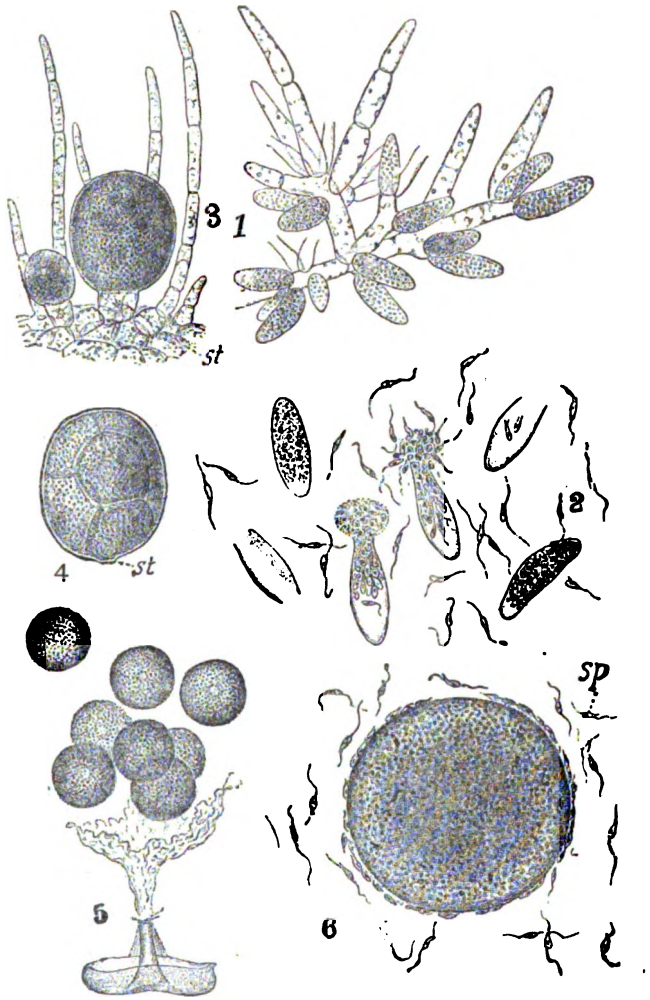


FIG. 360.—*Fucus*. *1*, Group of antheridia. *2*, Antheridia showing escaping spermatozoids. *3*, Oogonium, the contents of which have divided into eight egg-cells. *4*, Contents separated from stalk (*st*). *5*, Liberation of the egg-cells. *6*, Oosphere surrounded by spermatozoids. (After THURET. From OLTMANNS' *Algae*.)

somewhat elongated ovate bodies, having two lateral cilia of unequal length and a red eye-spot. The oogonia (Figs. 359 *o*; 360, 3) are nearly spherical, and are borne on a short stalk consisting of a single cell. They are of a yellowish-brown colour, and enclose eight spherical egg-cells which are formed by the division

of the oogonium mother cell and are separated by delicate cell walls. The eggs are enclosed within a thin membrane when ejected from the oogonium. This membranous envelope deliquesces at one end and, turning partly inside out, sets free the eggs (Fig. 360, 4, 5). The spermatozoids then gather round the eggs in such numbers that by the energy of their movements they often set them in rotation (Fig. 360, 6). After an egg has been fertilised by the entrance of one of the spermatozoids it becomes invested with a cell wall, attaches itself to the substratum, and gives rise by division to a new plant.

In the case of other Fucaceae which produce four, two, or even only one egg in their oogonia, the nucleus of each oogonium, according to OLTMANNS, nevertheless first divides into eight daughter nuclei, of which, however, only the proper number give rise to eggs capable of undergoing fertilisation. The other reduced eggs, incapable of fertilisation, degenerate.

Since the Fucaceae have no asexual spore-formation the alternation of generations characteristic of *Dictyota* is wanting in them. The thallus of *Fucus*, developed from the fertilised ovum, has diploid nuclei. Reduction takes place in the first two divisions within the oogonium and antheridium, so that four haploid nuclei result. In the oogonium one further division, and in the antheridium four take place before the sexual cells are produced. Thus in *Fucus*, in contrast to *Dictyota*, only a very short haploid stage can be recognised.

Economic Uses.—The dried stalks of *Laminaria digitata* and *L. Cloustoni* were used as dilating agents in surgery. IODINE is obtained from the ash (varec, kelp) of various Laminariaceae and Fucaceae, and formerly soda was similarly obtained. Many Laminarias are rich in MANNITE (*e.g. Laminaria saccharina*), and are used in its production, and also as an article of food by the Chinese and Japanese.

CLASS XI

Characeae (Stoneworts) ([1, 11, 48])

The Characeae or Charophyta form a group of highly organised green Thallophytes sharply isolated from both simpler and higher forms. Their origin must be looked for in the Chlorophyceae, but the complicated structure of their sexual organs does not allow of any immediate connection with the oogamous Green Algae. On the other hand, in certain characters they show some approach to the Brown Algae, from which they differ in the pure green colour of the chromatophores. They cannot be regarded as leading towards the Bryophyta although their karyokinetic nuclear division exhibits a great agreement with that of the Archegoniatae.

The Characeae grow in fresh or brackish water, attached to the bottom and covering extended areas with a mass of vegetation. Their regular construction and habit is characteristic. In some species the cylindrical main axes are over a foot in length, and are composed of long internodes alternating with short nodes, from which short cylindrical branches are given off in regular whorls with a similar structure, but of limited growth (Fig. 361). The lateral axes are either unbranched or give rise at their nodes to verticillate outgrowths of a second order. From the axil of one of the side branches of each whorl a lateral axis resembling the main axis is produced. The attachment to the substratum is effected by means of colourless branched rhizoids springing from the nodes at the base of the axes. The rhizoids

show a similar segmentation into long internodal cells and nodal cells that are laterally displaced. Branching takes place at the nodes.

Both the main and lateral axes grow in length by means of an apical cell, from which other cells are successively cut off by the formation of transverse walls. Each of these cells is again divided by a transverse wall into two cells, from the lower of which a long internodal cell develops without further division; while the upper, by continued division, gives rise to a disc of nodal cells, the lateral axes, and also, in the lower portion of the main axis, to the rhizoids. In the genus *Nitella* the long internodes remain naked, but in the genus *Chara* they become enveloped by a cortical layer consisting of longitudinal rows of cells which develop at the nodes from the basal cells of the lateral axes. A corresponding construction is found among other Thallophyta in certain Brown Algae (*e.g. Spermatochnus*).

FIG. 361.—*Chara fragilis*. End of main shoot. (Nat. size.)

Each cell contains one normal nucleus derived from a karyokinetic division. As a result of the fragmentation of its original nucleus, however, each internodal cell is provided with a number of nuclei which lie embedded in an inner and actively-moving layer of parietal protoplasm. Numerous round chloroplasts are found in the internodal cells.

Asexual reproduction by means of swarm-spores or other spores is unrepresented in the Characeae. Sexual reproduction, on the other hand, is provided for by the production of egg-cells and spermatozoids. The female organs are ovate. They are visible to the naked eye, and, like the spherical red-coloured antheridia, are inserted on the nodes of the lateral axes. With the exception of a few dioecious species, the Characeae are monoecious. The fertilised egg-cell develops into an oospore. The Characeae thus exhibit no alteration of generations but a succession of gametophytes.

The male organs (Fig. 362 *A*) are developed from a mother cell that first becomes divided into eight cells. Each octant by two tangential walls gives rise to three cells. In this way are derived the eight external tabular cells of the wall, the cavities of which are incompletely partitioned by septa extending in from the cell wall; the eight middle cells form the manubria and become elongated; the eight innermost cells assume a spherical form as the primary head cells. Owing to the rapid surface growth of the eight shield cells a cavity is formed within the male organ into which the manubria bearing the

head cells project. The latter form 3-6 secondary head cells, and from each of these arise 3-5 long unbranched spermatogenous filaments. These are composed of disc-shaped cells from each of which a spirally-wound spermatozoid with two cilia is liberated (Fig. 362 *C*). The spermatogenous filaments or antheridia may be compared morphologically to the plurilocular gametangia of the Brown Algae. These, as in *Stilophora* for instance, may consist of simple rows of cells and

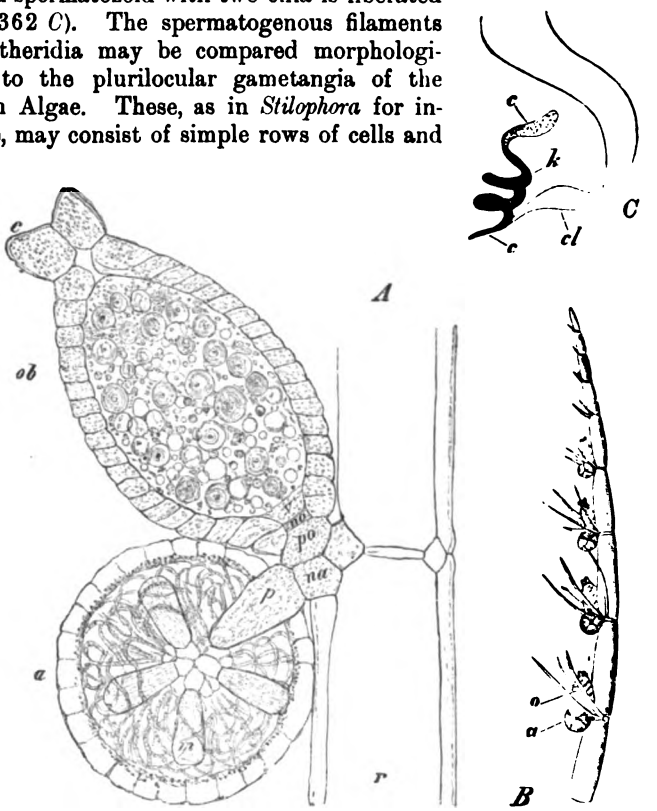


FIG. 362.—*Chara fragilis*. *A*, Median longitudinal section through a lateral axis *r*, and the sexual organs which it bears (× 60); *a*, antheridium borne on the basal nodal cell *na*, by the stalk cell *p*; *m*, manubrium; *ob*, an oogonium; *no*, nodal cell; *po*, the stalk cell; *v*, pivotal cell (*Wendungszelle*); *c*, the crown. *B*, A lateral axis (× 6); *a*, antheridium; *o*, oogonium. *C*, Spermatozoid; *k*, nucleus; *cl*, cilia; *c*, cytoplasm (× 540). (After STRASBURGER.)

be grouped together in sori. The male organ of the Characeae, which as a whole is commonly spoken of as an antheridium, thus contains eight groups of endogenously-formed antheridia and should on this account be termed an antheridiophore.

The female organ (Fig. 362 *ob*) consists of an oogonium which contains a single egg-cell with numerous oil-drops and starch grains. To begin with, the oogonium projects freely, but later becomes surrounded by five spirally-wound cells. These cells end in the corona,

between the cells of which the spermatozoids make their way in fertilisation. At the base of the oogonium there are small cells (*Wendungszellen*) cut off from the oogonial rudiment; in *Chara* there is one, in *Nitella* three such cells. These divisions correspond to the first divisions in the mother cell of the male organ. The female organ may thus be regarded as an oogoniophore reduced to a single oogonium.

The egg, after fertilisation, now converted into an oospore, becomes invested with a thick colourless wall. The inner walls of the tubes become thickened and encrusted with a deposit of calcium carbonate, while the external walls of the tubes, soon after the fruit has been shed, become disintegrated.

In the germination of the oospore the nucleus, according to OEHLKERS and ERNST, divides into four, the first division being heterotypic. The enlargement of the zygote opens the membrane at its summit. While three nuclei remain in the ventral portion of the zygote and there degenerate, the fourth nucleus enlarges and passes into the apical protrusion, which is then cut off by a cell wall. From this cell by further divisions a simple filamentous young plant consisting of a number of segments is produced. From the first node of this plant rhizoids are developed, while at the second some simple lateral axes arise as well as one or more main axes. By the further growth and branching of the latter the adult plant develops. The diploid stage in the Characeae is thus limited to the oospore, the plant itself being throughout haploid.

The behaviour of *Chara crinita* is remarkable. According to ERNST the haploid male and female individuals of this dioecious species only occur occasionally; their cells have twelve chromosomes. Diploid female plants with twenty-four chromosomes are, on the other hand, widely spread. These, which appear to have arisen by the crossing of *Chara crinita* with other species, are propagated apogamously by means of diploid egg-cells. This is therefore an example of apogamy and not, as was previously assumed, of parthenogenetic development of haploid egg-cells ([46a]).

The formation of tuber-like bodies (bulbils, starch-stars) on the lower part of the axes is characteristic of some species of the Characeae. These tubers, which are densely filled with starch and serve as hibernating organs of vegetative reproduction, are either modified nodes with much-shortened branch whorls (*e.g.* in *Tolypellopsis stelligera*, when they are star-shaped), or correspond to modified rhizoids (*e.g.* the spherical white bulbils of *Chara aspera*).

CLASS XII

Rhodophyceae (Red Algae) ([1, 11, 28, 49, 50])

The Rhodophyceae or Florideae constitute an independent group of the higher Algae, the phylogenetic origin of which is perhaps to be sought among the higher Green Algae, but they also exhibit connections with the Brown Algae. They are almost exclusively marine, and specially characterise the lowest algal region on the coasts of all oceans. A few genera (*e.g. Batrachospermum*, *Lemanea*) grow in fresh-water streams.

The thallus of the Red Algae exhibits a great variety of forms. The simplest forms are represented by branched filaments consisting of single rows of cells (*e.g. Callithamnion*). In other cases the branched filamentous thallus appears multicellular in cross-section. In many other forms the thallus is flattened and ribbon-like (*e.g. Chondrus crispus*, Fig. 363; *Gigartina mamillosa*, Fig. 364); while in other species it consists of expanded cell surfaces attached to a substratum. All the Florideae are attached at the base by means of rhizoidal filaments or discoid holdfasts. One of the more com-

FIG. 363.—*Chondrus crispus*. (½ nat. size.)

plicated forms is *Delesseria* (*Hydrolapathum*) *sanguinea* (Fig. 88), which occurs on the coasts of the Atlantic. The leaf-like thallus which springs from an attaching disc is provided with mid-ribs and lateral ribs. In the autumn the wing-like expansions of the thallus are lost, but the main ribs persist and give rise to new leaf-like branches in the succeeding spring. The thalli of the Corallinaceae, which have the form of branch-systems or of flattened or tuberculate incrustations, are especially characterised by their coral-like appearance, owing to the large amount of calcium carbonate deposited in their cell walls. The calcareous Florideae are chiefly found on coasts exposed to a strong surf, especially in the tropics.

The Rhodophyceae are usually red or violet; sometimes, however, they have a dark purple or reddish-brown colour. Their chromatophores, which are flat, discoid, oval, or irregular-shaped bodies and closely crowded together in large numbers in the cells, contain a red pigment, PHYCOERYTHRIN, and in some cases a blue pigment (PHYCOCYAN) in addition. They are developed from colourless, spindle-shaped leucoplasts in the apical cells and germ cells. True starch is never formed as a product of assimilation, its place being taken by other substances, very frequently, for example, by Floridean starch in the form of spherical stratified grains which stain red with iodine. Oil-drops also occur. The cells may contain one or several nuclei.

Reproduction is effected either asexually by means of spores, or sexually by the fertilisation of female organs by male cells.

FIG. 364.—*Gigartina mamillosa*. *s*, Wart-shaped cystocarps. (½ nat. size.)

The asexual SPORES are of two kinds. In the first case they are non-motile, have no cilia, and are simply naked spherical cells. They are produced, usually, in groups of four, by the division of a mother cell or sporangium. The sporangia themselves are nearly spherical or oval bodies seated on the thalloid filaments or embedded in the thallus. The spores escape by a transverse rupture of the wall of the sporangium. In consequence of their usual formation in fours, the spores of the Florideae are termed TETRASPORES (Fig. 365). They are analogous to the swarm-spores of other Algae; similar spores are found also in the Dictyotaceae among the Brown Algae. The tetrasporangium as a rule has to begin with a single nucleus, which divides to give rise to the nuclei of the four spores. In some cases (*Martensia*, *Nitophyllum*), however, they are to begin with multinucleate, but all the nuclei except one degenerate. The monosporangia of the Nemalionaceae, which liberate only a single spore, and the polysporangia of the Ceramiaceae, which form a number, are equivalent to the tetrasporangia.

The second form of asexual spore in the Red Algae is represented by the CARPOSPORES (cf. p. 424), which are liberated singly from terminal carposporangia as spherical and, to begin with, naked, non-ciliate protoplasts, and thus resemble the monospores.

In the construction of the sexual organs, particularly the female, the Rhodophyceae differ widely from the other Algae. *Batrachospermum moniliforme*, a fresh-water form, may serve as an example to illustrate the mode of their formation. This Alga possesses a brownish thallus, enveloped in mucilage, and consisting of verticillately-branched filaments. The sexual organs appear on the branching whorls seated on closely-crowded, short, radiating branches.

The antheridia, also known as spermatangia (Fig. 366 *A*), are produced

usually in pairs, at the ends of the radiating branches. Each antheridium consists of a single thin-walled cell, in which the whole of the protoplasm is consumed in the formation of one uninucleate SPERMATIUM; in *Batrachospermum* and *Nemalion* the nucleus of the spermatium divides into two. The spermatia are nearly spherical, and are invested with a thin outer membrane or cell wall. They are non-motile, unlike the ciliated spermatozoids of the other Algae, and have therefore received a distinctive name. In consequence of their incapacity for independent movement, they must be carried passively by the water to the female organs, which are situated near the antheridia at the ends of other branches. The female organ is called a CARPOGONIUM (Fig. 367), and consists of an elongated cell with a basal flask-shaped portion prolonged into a filament, termed the TRICHOGYNE. The basal portion contains the nucleus of the egg and the chromatophores, while the trichogyne functions

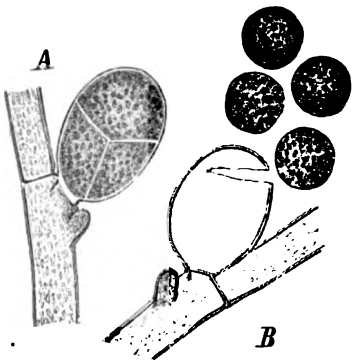


FIG. 365.—*Callithamnion corymbosum*. *A*, Closed sporangium; *B*, empty sporangium with four extruded tetraspores. (After THURET.)

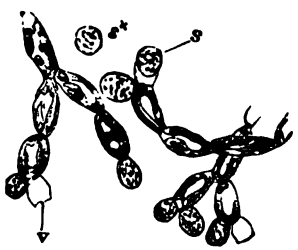


FIG. 366. — *Batrachospermum moniliforme*. Branches bearing antheridia. At *s**, a free spermatium; at *s*, another just escaping; at *v*, an empty antheridium. (× 540. After STRASBURGER.)

as a receptive organ for the spermatia, one or two of which fuse with it, and the contents, escaping through the spermatium wall, pass into the carpogonium. The sperm nucleus passes down the trichogyne and fuses with the nucleus of the egg-cell. The fertilised egg, which becomes limited from the trichogyne by a wall, does not become converted directly into an oospore, but, as a result of fertilisation, numerous branching sporogenous filaments (GONIMOBLASTS) grow out from the sides of the ventral portion of the carpogonium. At the same time, by the development of outgrowths from cells at the base of the carpogonium an envelope is formed about the sporogenous filaments. The whole product of fertilisation, including the surrounding envelope, constitutes the fructification, and is termed a CYSTOCARP. The profusely-branched sporogenous filaments become swollen at the tips and give rise to spherical, uninucleate spores known as CARPOSPORES, which are eventually set free from the envelope. In the case of *Batrachospermum* the carpospores produce a filamentous protonema, the terminal cells of which give rise to asexual unicellular spores. These spores serve only for the multiplication of the protonema. Ultimately, however, one of the lateral branches of the protonema develops into the sexually differentiated filamentous thallus. The production of spores by the protonema is analogous to the formation of tetraspores by other Florideae.

The homologies underlying the variously-constructed sexual organs of the Red

Algae can be recognised, according to N. SVEDELIUS, when their development is taken into consideration and they are compared in the light of the first nuclear division in the rudiment. The young carpogonium contains two nuclei, of which that belonging to the trichogyne later degenerates. (The uninucleate carpogonium of *Batrachospermum* is apparently an exception.) The trichogyne corresponds morphologically to the spermatangium, and its ventral portion to the basal or mother cell on which one or more spermatangia are situated. The trichogyne and egg-cell are only separated by a cell wall after fertilisation ([49b]).

The formation of the antheridia ([49a]) as well as of the frequently very complicated cystocarps follows a variety of types in the Florideae. In all cases, however, according to OLTMANNS, the carpospores are to be regarded as derived in their development from the fertilised egg-cell.

Dudresnaya coccinea, which is found on the warmer coasts of Europe, has a

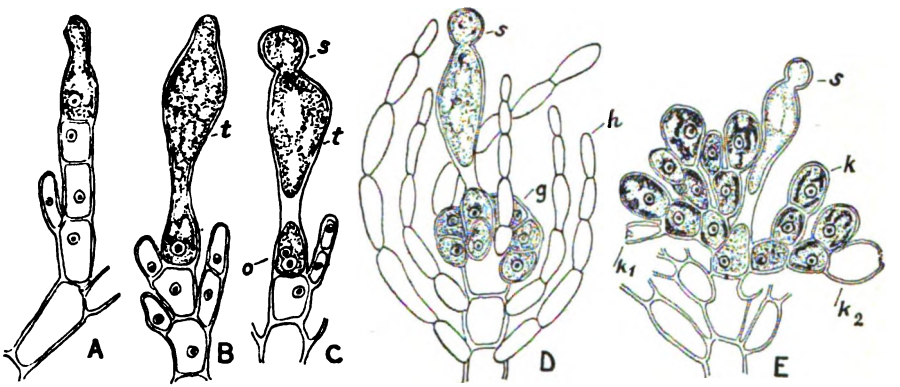


FIG. 367. — *Batrachospermum moniliforme*. *A*, Young carpogonium terminating a branch. *B* Ripe carpogonium; *t*, trichogyne. *C*, Stage after fertilisation by the spermatium (*s*), the egg, cell (*o*) containing the two sexual nuclei. *D*, Gonimoblasts (*g*) and investing filaments (*h*). *E*, Some of the mature gonimoblasts with the carpospores (*k*); these have emerged from k_1 and k_2. (*A*-*D* × 960, *E* × 720. After H. KYLIN.)

branched, cylindrical thallus and will serve as an example of the more complicated mode of origin of the spore-bearing generation (Fig. 368). The carpogonial branches consist of about seven cells, the terminal one bearing a very long trichogyne. After fertilisation the carpogonial cell grows out into a filament, which elongates and becomes branched. This filament fuses with a number of special cells, characterised by their abundant contents, the AUXILIARY CELLS. The first of these lie in the carpogonial branch itself, the others in adjoining lateral branches. All the nuclei of the sporogenous filament are derived by division from that of the fertilised egg-cell. The successive fusions with auxiliary cells do not involve nuclear fusions, but simply serve to nourish the sporogenous filament. A second and third sporogenous filament may arise from the carpogonial cell. Two outgrowths now arise from each of the swollen cells of the sporogenous filament which fused with auxiliary cells. By further division of these outgrowths the spherical masses of carpospores, which subsequently become free, are derived.

In all Red Algae, as has been seen above, two generations can be distinguished, the GAMETOPHYTE, which produces the egg-cells and the spermatia, and the SPOROPHYTE, which proceeds from the fertilised egg and produces the carpospores

asexually. The two differ from one another in form, the gametophyte being an

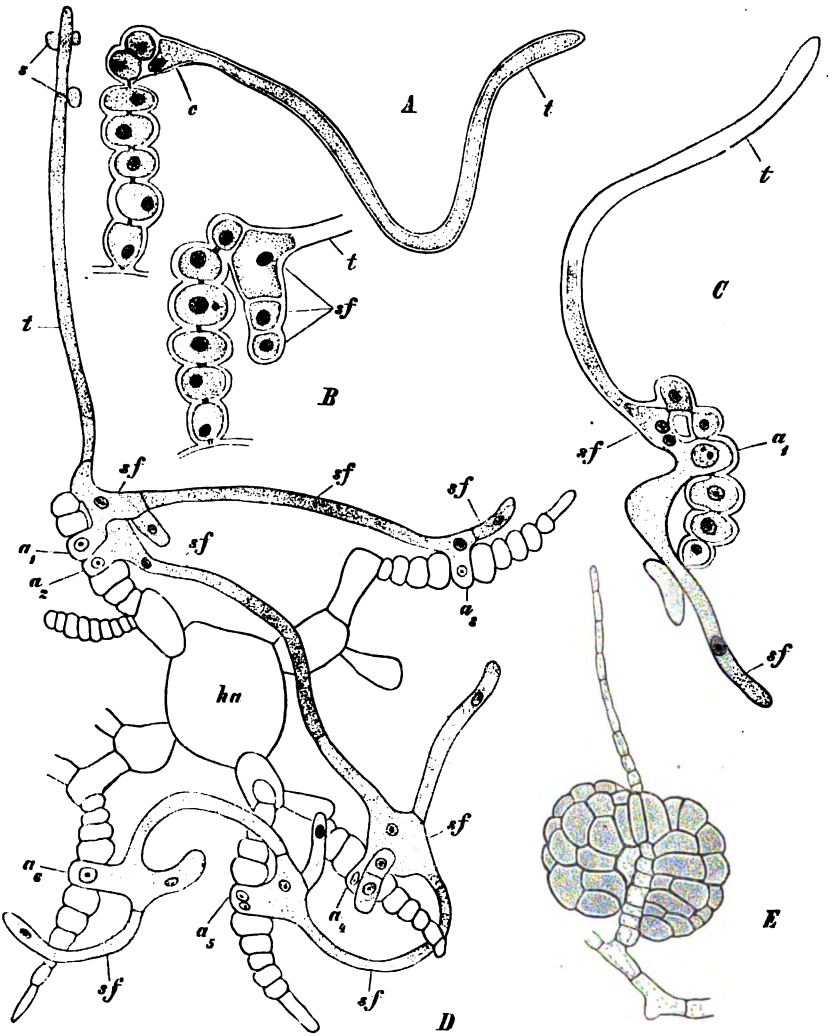


FIG. 368.—*Dudresnaya coccinea*. *A*, Carpogonial branch ; *c*, carpogonium ; *t*, trichogyne. *B*, Carpogonium after fertilisation, grown out into the sporogenous filament (*sf*). *C*, Fusion of the sporogenous filament with the first auxiliary cell (a_1). *D*, Branching of the filament and fusion with six auxiliary cells (a_1-a_6) ; the cells a_3-a_6 are borne on branches originating from the axis *ha* (diagrammatic). *E*, Ripe cluster of carpospores originating from one branch. (*A-D* after OLTMANNS ; *E* after BORNET. *A-C* × about 500 ; *D* × 250 ; *E* × 300.)

independent plant, while the sporophyte is morphologically more primitive and is dependent in its nutrition and development upon the sexual plant.

The spores produced in the tetrasporangia (or in the corresponding monosporangia or polysporangia) represent a second form of asexual spore, by means of which an increase in numbers of the sexual plants is effected. They may be entirely wanting in some cases (*Nemalion*).

In certain genera these sporangia occur only on the sexual plant itself. In the majority of genera, on the other hand, plants are developed from the carpospores which bear tetraspores only, and from these tetraspores the, usually dioecious, sexual plants arise. The life-history then includes the three generations, gametophyte, carposporophyte, and tetrasporophyte. A purely asexual generation morphologically resembling the sexual generation has here been secondarily derived from the latter. In some Red Algae with such a life-history a further complication is introduced by the gametophyte bearing tetraspores, or equivalent monospores, which again produce gametophytes.

The behaviour of the nuclei and their reduction division has been investigated in a small number of species and has revealed noteworthy differences in the distribution of the haploid and diploid phases among the generations ([49c]).

In *Scinaia* the reduction division, according to SVEDELIUS, takes place in the first division of the fertilised egg, so that this only is diploid while the carposporophyte, the carpospores, and the gametophyte proceeding from the latter are all haploid. The gametophyte here reproduces itself asexually by haploid monospores in place of tetraspores, which are wanting. *Nemalion*, according to KYLIN, behaves similarly but has neither tetraspores nor monospores on the gametophyte.

It may be anticipated that in all Red Algae with this simple alternation of generations the reduction division will follow the *Scinaia* type, which can be regarded as the most primitive.

In those Red Algae in which three generations occur in the life-history the reduction division is relegated to the tetrasporangium, so that the gametophyte proceeding from the tetraspores is haploid, while the carposporophyte, the carpospores, and the tetrasporophyte developed from the latter constitute the diploid phase. *Polysiphonia*, *Griffithia*, *Delesseria*, *Nitophyllum*, and *Rhodomela* are known to behave in this way. If in such cases asexual spore-formation takes place on the gametophyte this does not involve a reduction division. According to SVEDELIUS the gametophyte of *Nitophyllum punctatum* is an example of this; it bears monospores in addition to the sexual organs. These monosporangia correspond to the tetrasporangia of the tetrasporophyte, are at first multinucleate, but all the nuclei except one degenerate. They produce, without any reduction, a single, haploid monospore.

Harveyella mirabilis ([50]), one of the Florideae occurring in the North Sea, is of special interest. It grows as a parasite on another red seaweed, *Rhodomela subfusca*, on which it appears in the form of a small white cushion-like growth. As a result of its parasitic mode of life the formation of chromatophores has been entirely suppressed, and thus this plant behaves like a true fungus.

Economic Uses.—*Gigartina mamillosa* (Fig. 364), with peg-like cystocarps 2-5 mm. in length, and *Chondrus crispus* (Fig. 363), with oval cystocarps about 2 mm. long, sunk in the thallus and tetraspores in groups on the terminal segments of the thallus. Both forms occur in the North Sea as purplish-red or purplish-brown Algae; when dried they have a light yellow colour, and furnish the official CARRAGHEEN, "Irish Moss," used in the preparation of jelly. AGAR-AGAR, which is used for a similar purpose, is obtained from various Florideae; *Sphaerococcus* (*Gracilaria*) *lichenoides* supplies the Agar of Ceylon (also called Fucus amylaceus),

Eucheuma spinosum the Agar of Java and Madagascar, *Gelidium corneum* and *G. cartilagineum* the Agar of Japan.

Class XIII

Phycomycetes ([1, 51, 52, 53-60])

In the structure both of their thallus and sexual organs the Phycomycetes exhibit a close connection with the Siphoneae. The phylogenetic origin of most of the Phycomycetes is probably to be sought in this group, though certain forms point to a relationship with other Green Algae (*e.g. Basidiobolus* with the Conjugatae, and the Chytridiaceae with Protococcales and Flagellata). They can only for the present be regarded as a definite class, pending their separation into several series derived from distinct classes of Algae.

In the simplest cases, as in the Chytridiaceae, the thallus consists of a single cell which in its young stages is a naked protoplast. In the higher forms the thallus consists of extensively-branched tubular threads in which, as is the case in *Vaucheria*, transverse septa only form in connection with the reproductive organs. The continuous protoplasmic mass contains numbers of very small nuclei, but chromatophores are entirely wanting in these colourless organisms. The whole thallus of a fungus is spoken of as the MYCELIUM, the individual filaments as HYPHAE. In the Phycomycetes the hyphae are non-septate, their division into distinct cells only taking place in a few cases. The plants are either saprophytes occurring on the putrefying remains of animals or plants in water or on decaying organic substances exposed to air, or they live parasitically in the tissues of higher plants or of insects.

Asexual reproduction is effected by means of spores. These are formed in the majority of the genera within sporangia, the protoplasm of which splits into the numerous spores. The latter escape in the genera which live in water as ciliated swarm-spores (Fig. 371); in the forms which are exposed to the air the spores are enclosed by a cell wall (Fig. 377). The conidia, which are sometimes found together with sporangia, in other cases alone, are also adapted for dispersal in air. They arise by a process of budding and abstriction from the ends of certain hyphae which are usually raised above the substratum as special conidiophores.

The sexual organs of the Phycomycetes are in many ways peculiar, and the two groups of the Oomycetes and the Zygomycetes are distinguished according to their nature. In the Oomycetes, which stand nearest to the Siphoneae, oogonia and antheridia are found; the contents of the latter enter the oogonium by means of a tubular outgrowth, and after fertilisation oospores are formed. In *Monoblepharis* alone free spermatozoids are found. The sexual organs of the Zygomycetes are alike, and on conjugation a zygospore

is produced. They are usually multinucleate, and thus are morphologically comparable to a whole gametangium of an isogamous Alga. In the Archimycetes sexual organs have been observed in a few cases only in the form of antheridia and oogonia or of equivalent gametes.

Multinucleate gametangia, oogonia, and antheridia, which fuse directly with one another, without the separation and escape of the individual gametes, are generally termed COENOGAMETES.

Order 1. Archimycetes (53)

The **Chytridiaceae** which belong here are microscopically small Fungi parasitic on aquatic or land plants and in some cases on animals. The non-septate mycelium is feebly developed, and is frequently reduced to a single sac-shaped cell inhabiting a cell of the host. Asexual multiplication is effected by means of swarm-spores provided with one or two cilia which enter the cells of the host plant and at first have no cell wall. A cell wall is then formed and the parasite becomes transformed into a multinucleate sporangium which liberates numerous uninucleate swarm-spores by means of a beak-like projection. Thick-walled sporangia which only produce swarm-spores after a period of rest are also developed. The life-history of *Olpidium Brassicae* (Fig. 369), which lives as a parasite in the stems of young Cabbage plants and causes their death, is of this type. *Synchytrium* (*Chrysophlyctis*) *endobioticum*, the cause of the wart disease of the Potato, has recently become widespread in Europe. It gives rise to warty outgrowths on the stems and tubers; these later break down and decay. In summer it forms from the protoplast a sorus of 2-5 spherical, thin-walled sporangia without beak-like projections, and also especially for the winter rest, thick-walled, yellow, resting sporangia. These are at first uninucleate, but on germinating in the moist soil form numerous uniciliate swarm-spores which can enter the cells of the Potato.

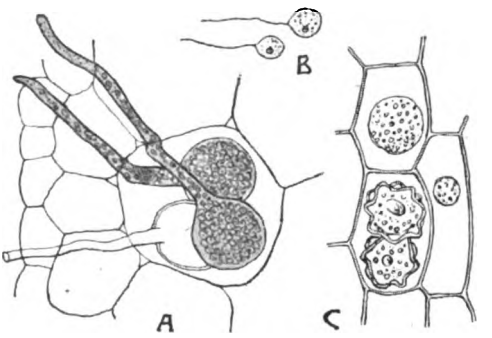


FIG. 369.—*Olpidium Brassicae*. *A*, Three zoosporangia, the contents of one of which has escaped (× 160). *B*, Zoospores (× 520). *C*, Resting sporangia (× 520). (After WORONIN.)

Sexual reproduction as a preliminary to the formation of resting sporangia is only known with certainty for a few forms. In *Olpidium Viciae*, which is parasitic on *Vicia unijuga*, the uniciliate swarm-spores are in part asexual, producing zoosporangia again a few days after entering a cell of the host. In part, however, they behave as planogametes and conjugate in pairs to form naked zygotes provided with two cilia. The zygote settles on the host plant, surrounds itself with a cell wall and passes its protoplast into the epidermal cell. Within this the zygote develops into a resting sporangium, in which the delayed fusion of the sexual nuclei takes place; from this, numerous zoospores are developed.

In *Olpidiopsis*, which is parasitic in the hyphae of *Saprolegnia*, the method of conjugation is different and more like that of the higher Phycomycetes. Larger female and smaller male protoplasts lie side by side in the host cells, where they grow, become multinucleate, and surround themselves with cell walls. The contents of the male cell now pass into the female cell, which becomes a thick-walled oospore. The nuclei appear to fuse in pairs. The further fate of this oospore is not known. *Olpidiopsis* also multiplies by biciliate zoospores formed in sporangia.

In other genera no sexuality has yet been demonstrated and no conjugation precedes the development of the resting sporangia.

Order 2. Oomycetes

1. Only in the small primitive family of the **Monoblepharideae** ([54]) are free ciliated spermatozoids liberated from the antheridia. In the other Oomycetes the

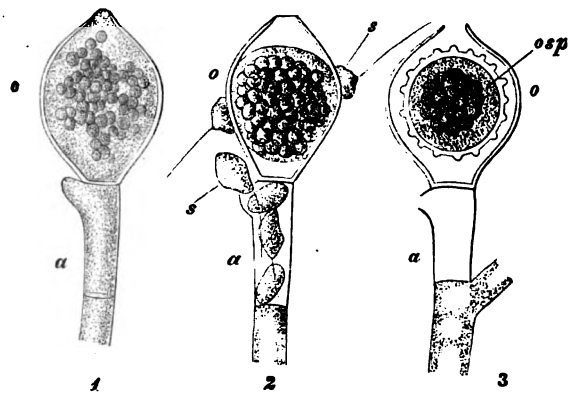


FIG. 370.—*Monoblepharis sphaerica*. End of filament with terminal oogonium (*o*) and an antheridium *a*). *1*, Before the formation of the egg-cells and spermatozoids. *2*, Spermatozoids (*s*) escaping and approaching the opening of the oogonium. *3*, *osp*, ripe oospore, and an empty antheridium. (× 800. After CORNU.)

multinucleate contents of the antheridium do not divide into separate spermatozoids.

The species of *Monoblepharis* live in water upon decaying remains of plants. Asexual reproduction is effected by means of uniciliate swarm-spores, formed in large numbers in sporangia. The oogonium, which is usually terminal, contains only a single egg-cell (Fig. 370). The antheridia, which resemble the sporangia, liberate a number of uniciliate spermatozoids. On a spermatozoid reaching the egg-cell through an opening in the tip of the oogonium an oospore is formed. A spinous cell wall forms around the oospore.

2. The **Saprolegniaceae** ([55]), which connect on to the preceding family, live like them saprophytically on the surface of decaying plants and insects and even on living fishes. Asexual propagation is effected by club-shaped sporangia (Fig. 371) which produce numerous biciliate swarm-spores. In *Saprolegnia* these swarm-spores with terminal cilia withdraw the latter and become surrounded with a spherical wall; shortly afterwards, the contents again escape as bean-shaped zoospores with the cilia inserted laterally. The sexual organs develop on older branches of

the mycelium (Figs. 372, 373). The oogonia give rise to a larger (as many as 50) or smaller number of egg-cells, rarely only to a single one. At first the oogonium contains numerous nuclei, most of which, however, degenerate; the remaining nuclei divide once mitotically into daughter nuclei, of which some again degenerate, while the oospheres become delimited around the remaining nuclei. The egg-cells are always uninucleate. The tubular antheridia, with a number of nuclei that undergo one mitotic division, apply themselves to the oogonia and send fertilising tubes to the egg-cells. One male nucleus enters the egg-cell and fuses with its nucleus. The oospore after fertilisation acquires a thick wall. The reduction division takes place on the germination of the oospore. In some forms belonging to this

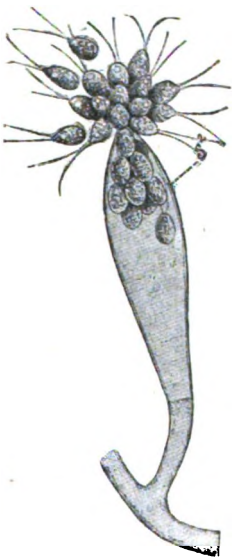


FIG. 371.—*Saprolegnia mixta*. The biciliate zoospores, *s*2, are escaping from the sporangium. (After G. KLEBS.)

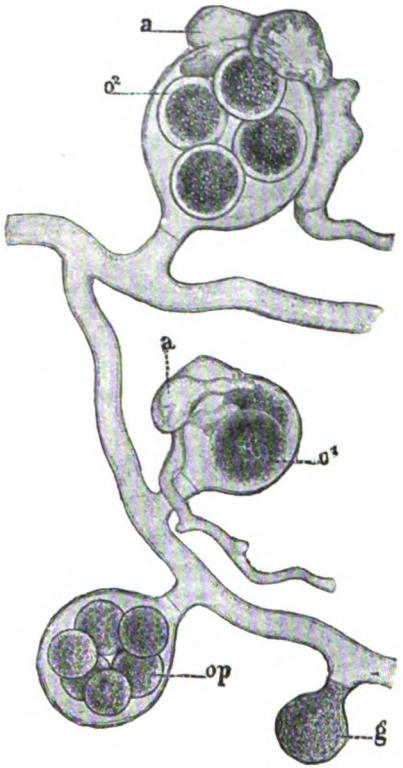


FIG. 372.—*Saprolegnia mixta*. Hyphae bearing the sexual organs: *a*, antheridium which has sent a fertilisation tube into the oogonium; o^1, egg-cell; o^2, oospore enclosed in a cell wall; *op*, parthogenetic oospores; *g*, young oogonium. (After G. KLEBS.)

family, and also in some Peronosporeae, the formation of antheridia is occasionally or constantly suppressed; the oospores develop parthenogenetically without being fertilised (Fig. 372 *op*).

3. The **Peronosporeae** (56) are parasitic fungi whose mycelium penetrates the tissues of the higher plants. In damp climates certain species occasion epidemic diseases in cultivated plants. Thus, the mycelium of *Phytophthora infestans*, the fungus which causes the Potato disease, lives in the intercellular spaces of the leaves and tubers of the Potato plant, and by penetrating the cells with its short

haustoria leads to the discoloration and death of the foliage and tubers. Sexual reproductive organs have not as yet been observed in this species on the Potato plant but have been produced when the fungus is cultivated on certain media. Asexual, oval sporangia are formed on long branching sporangiophores which grow out of the stomata, particularly from those on the under side of the leaves (Fig. 374), and appear to the naked eye as a white mould. The sporangia, at first terminal, are cut off by transverse walls from the ends of the branches of the sporangiophore, by the subsequent growth of which they become pushed to one side, and so appear to be inserted laterally. Before any division of their contents has taken place, the sporangia (*B*) fall off and are disseminated by the wind; in this way the epidemic becomes widespread. The development of swarm-spores in sporangia is effected only in water, and is consequently possible only in wet weather. In this process the contents of the sporangium divide into several biciliate swarm-spores

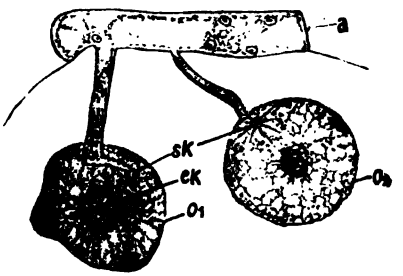


FIG. 373.—*Achlya polyandra*. The fertilisation of two egg-cells, *o*, of an oogonium by two tubes from the antheridium, *a*; *ek*, nucleus of the egg-cell; *sk*, sperm-nucleus; in o_2 the section has not passed through the egg-nucleus. (After TROW.)

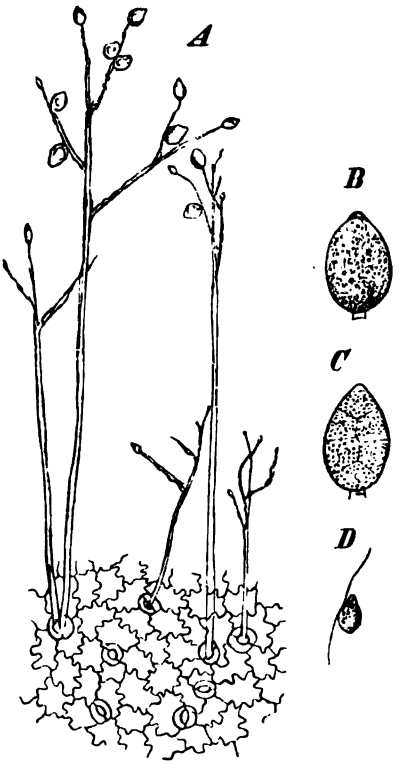


FIG. 374.—*A*, Surface view of the epidermis of a potato leaf, with sporangiophores of *Phytophthora infestans* projecting from the stomata (× 90); *B*, a ripe sporangium; *C*, another in process of division; *D*, a swarm-spore. (*B-D* × 540. After STRASBURGER.)

(*C*, *D*). Each of these spores, after escaping from the sporangium, gives rise to a mycelium, which penetrates the tissues of a leaf. The sporangium may also germinate directly without undergoing division and forming swarm-spores. A similar transformation of sporangia into conidia is also found in other Peronosporeae as a result of their transition from an aquatic to a terrestrial mode of life.

Plasmopara viticola, an extremely destructive parasite, also produces copiously-branched sporangiophores and occasions the "False Mildew" of the leaves and fruit of the Grape-vine. *Albugo candida* (= *Cystopus candidus*), another very common species, occurs on Cruciferae, in particular on *Capsella bursa pastoris*, causing white swellings on the stems. In this species the sporangia are formed in long

chains on the branches of the mycelium under the epidermis of the host plant, and produce in water numerous swarm-spores.

The sexual organs of the Peronosporeae resemble those of the genus *Vaucheria* (Fig. 348). They arise within the host plant—the oogonia as spherical swellings of the ends of certain hyphae, the antheridia as tube-like outgrowths arising as a rule just below the oogonia. Both are cut off by transverse walls and are multinucleate (Fig. 375). The several species exhibit interesting differences as regards the nuclear changes. In *Peronospora parasitica*, *Albugo candida*, and *A. Lepigoni*, *Pythium*, *Plasmopara*, and *Sclerospora*, a single large central egg-cell or oosphere becomes differentiated in the protoplasm of the oogonium; this contains a

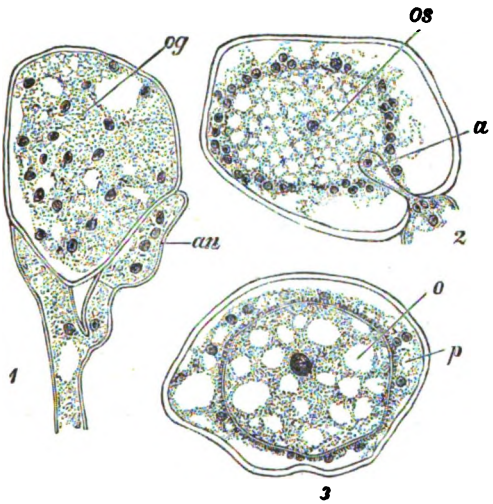


FIG. 375.—Fertilisation of the Peronosporeae. *1*, *Peronospora parasitica*. Young multinucleate oogonium (*og*) and antheridium (*an*). *2*, *Albugo candida*. Oogonium with the central uninucleate oosphere and the fertilising tube (*a*) of the antheridium which introduces the male nucleus. *3*, The same. Fertilised egg-cell (*o*) surrounded by the periplasm (*p*). (× 666. After WAGER.)

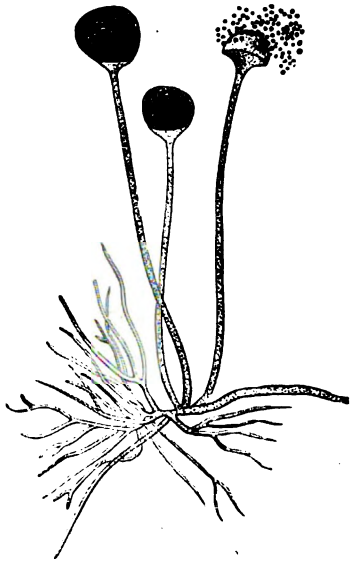


FIG. 376. — *Rhizopus nigricans* (= *Mucor stolonifer*). Portion of the mycelium with three sporangia; that to the right is shedding its spores and shows the persistent hemispherical columella. (× 38.)

single nucleus in a central position, while the remaining nuclei pass into the peripheral layer of protoplasm (periplasm). The antheridium now sends a process into the oogonium, which at its apex opens into the oosphere and allows a single male nucleus to pass into the latter. The oosphere then becomes surrounded with a cell wall, and nuclear fusion takes place, while the periplasm is utilised in forming the outer membrane of the spore (episporium). In *Peronospora parasitica* the ripe oospore has a single nucleus, in *Albugo* it becomes multinucleate as a result of nuclear division. In *Albugo Bliti* and *A. portulacae* there is also a central oosphere surrounded by periplasm, but the oosphere contains numerous nuclei, which fuse in pairs with a number of male nuclei entering from the antheridium. A multinucleate oospore thus arises from the compound egg-cell. The behaviour of these two species can be regarded as primitive, the uninucleate oospheres of

the first-named forms having been derived from the multinucleate condition. *Albugo tragopogonis* occupies an intermediate position in that its oosphere is at first multinucleate, but later contains only one female nucleus, the others having degenerated. The superfluous nuclei in the oogonia and antheridia may be regarded as the nuclei of gametes which have become functionless, and are comparable with the superfluous egg-nuclei of certain Fucaceae. The oospores either produce a mycelium directly or give rise to swarm-spores. The nuclei in the oospore are diploid; their first division, which may occur before germination, is the reduction division.

Order 3. Zygomycetes

1. The **Mucorineae** [57] comprise a number of the most common Mould Fungi. They are terrestrial and saprophytic, and are found chiefly on decaying vegetable and animal substances. Asexual reproduction is effected by non-motile, walled spores, which either have the form of conidia or arise endogenously in sporangia.

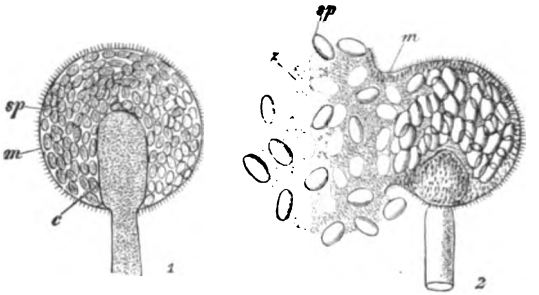


FIG. 377.—*1*, *Mucor Mucedo*. A sporangium in optical longitudinal section; *c*, columella; *m*, wall of sporangium; *sp*, spores. *2*, *Mucor mucilagineus*. A sporangium shedding its spores; the wall (*m*) is ruptured, and the mucilaginous substance (*z*) between the spores is greatly swollen. (1 × 225, 2 × 300, from v. TAVEL, *Pilze*. After BREFELD.)

Sexual reproduction consists in the formation of zygospores, as a result of the conjugation of two equivalent coenogametes.

One of the most widely distributed species is *Mucor Mucedo*, frequently found forming white fur-like growths of mould on damp bread, preserved fruits, dung, etc. *Mucor stolonifer* (= *Rhizopus nigricans*), with a brown mycelium, occurs on similar substrata. The spherical sporangia are borne on the ends of thick, erect branches of the mycelium (Fig. 376). From the apex of each sporangiophore a single spherical sporangium is cut off by a transverse wall, which protrudes into the cavity of the sporangium and forms a columella (Fig. 377). The contents of the sporangium become divided by repeated cleavages into numerous spores. These escape by the swelling of a substance which lies between the spores and the bursting of the sporangial wall. In *Pilobolus*, which occurs commonly on dung, the sporangium is forcibly cast off from the turgid sporangiophore which bursts at the columella (cf. pp. 349, 350). According to HARPER the spores of *Pilobolus* are binucleate, while those of *Sporodinia* (Fig. 378) are multinucleate.

Under certain conditions, instead of asexual sporangia, organs of sexual reproduction are produced. The hyphae of the mycelium then give rise to lateral, club-shaped branches. When the tips of two such branches come into contact, a conjugating cell or coenogamete is cut off from each by a transverse wall (Fig. 379). The two gametes thereupon coalesce, and fuse into a ZYGOSPORE, the outer wall of

which is covered with warty protuberances. As regards the behaviour of the nuclei in the process of conjugation, only a few facts are known. In *Sporodinia*, *Phycomyces*, and other genera the sexual nuclei in the zygospore fuse in pairs. After a period of rest the zygospore germinates, developing a germ-tube, which may at once bear a sporangium (Fig. 379, 5). The reduction division in *Phycomyces* takes place, according to BURGEFF, in the young sporangium formed on the germ-tube of the zygospore.

BLAKESLEE'S demonstration of the dioecious (heterothallic) nature of the mycelium of most Mucorineae, for example *Mucor Mucedo* and *Rhizopus nigricans*, is of great interest. The formation of zygospores only takes place when male and female mycelia come in contact. In other Mucorineae (homothallic, *e.g. Sporodinia grandis*) the two conjugating gametes may arise on the same mycelium. Exceptionally in heterothallic species, such as *Phycomyces nitens*, a homothallic mycelium may appear or a neutral mycelium which forms sporangia only [57a].

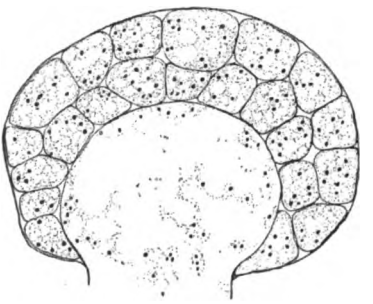


FIG. 378.—*Sporodinia grandis*. Median section of a ripe sporangium. The spores are multinucleate. (× 425. After HARPER.)

Within the group of the Zygomycetes a reduction of sexuality can be seen. Thus, in the case of certain Mucorineae, although the conjugating hyphae meet in pairs, no fusion takes place, and their terminal cells become converted directly into spores, which are termed AZYGOSPORES. In other forms, again, hyphae-producing azygospores are developed, but remain solitary, and do not, as in the preceding case, come into contact with similar hyphae. There are also many species in which the formation of zygospores is infrequent.

Both the size and number of spores produced in the sporangia of *Mucor Mucedo* are subject to variation. The sporangia of the genus *Thamnidium* are, on the other hand, regularly dimorphic, and a large sporangium containing many spores is formed at the end of the main axis of the sporangiophore, while numerous small sporangia, having but few spores (sporangioles), are produced by its verticillately branching lateral axes. The sporangia may at times develop only a single spore, as the result of certain conditions of food-supply, and in this way assume the character of conidia. This dimorphism is even more complete in the tropical genus *Choanephora*. In this case, in addition to large sporangia, conidia are produced on special conidiophores. There are, finally, Zygomycetes (*e.g. Chaetocladium*) whose only asexual spores are conidia. In this one group, therefore, all transitional forms, from many-spored sporangia to unicellular conidia, are represented.

Rhizopus nigricans has a poisonous substance in its cell sap which has fatal effects on animals [58].

2. The **Entomophthorineae** [59] is a small group of fungi which mostly live parasitically in the bodies of insects and caterpillars. The multinucleate mycelium remains non-septate or later becomes divided into cells. Asexual multiplication is effected by means of conidia which contain one or numerous nuclei. These arise singly at the ends of branches of the mycelium and when ripe are forcibly abjected. Sexual reproduction is by means of zygospores, in place of which azygospores frequently arise.

The best-known example is *Empusa muscae* (Fig. 380), which is parasitic on house-flies. The conidia, which are multinucleate, form a white halo around the

body of the dead fly which has been killed by the fungus. This is particularly well seen when the dead fly is adhering to the glass of a window.

3. **Basidiobolaceae** (60).—*Basidiobolus ranarum*, a saprophytic fungus growing on the excrement of Frogs, must be separated from the preceding group. Each of the cells of its septate mycelium contains one large nucleus. The conidia, which arise singly on the ends of the conidiophores and are abjected when ripe, are uninucleate. The mode of origin of the zygospores is peculiar. Two adjoining cells

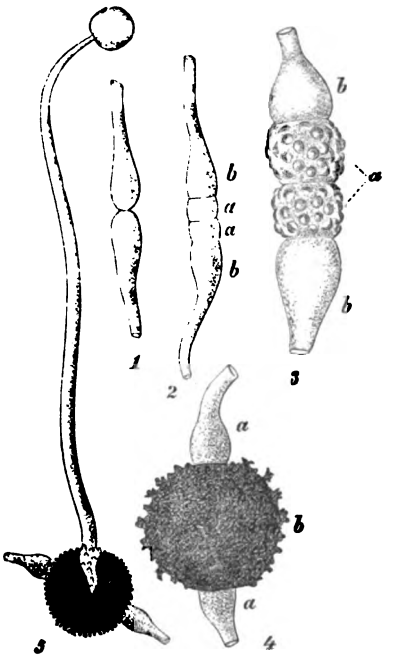


FIG. 379.—*Mucor Mucedo*. Different stages in the formation and germination of the zygospore. *1*, Two conjugating branches in contact; *2*, septation of the conjugating cells (*a*) from the suspensors (*b*); *3*, more advanced stage, the conjugating cells (*a*) are still distinct from one another: the warty thickenings of their walls have commenced to form; *4*, ripe zygospore (*b*) between the suspensors (*a*); *5*, germinating zygospore with a germ-tube bearing a sporangium. (1-4 × 225, 5 × circa 60, from v. TAVEL, *Pilze*. After BREFELD.)

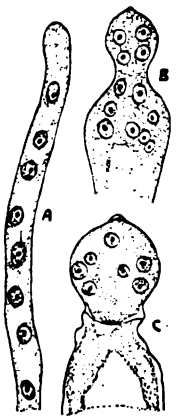


FIG. 380.—*Empusa muscae*. *A*, Hypha from the body of a fly. *B*, Young conidiophore arising from the mycelium and projecting from the body of the insect. *C*, Formation of the conidium into which the numerous nuclei have passed from the conidiophore. (× 450. After OLIVE.)

conjugate after they have put out beak-shaped processes which are cut off as transitory cells. In the zygospore the two sexual nuclei give rise to four, of which two disorganise while the other two fuse. Both in this procedure and in the nuclear structure there are evident resemblances to the Conjugatae.

CLASS XIV

Eumycetes (1, 51, 52, 61-86)

When the Phycomycetes are excluded there remain two great groups of Fungi, the Ascomycetes and the Basidiomycetes, regarding

the classification and phylogeny of which there is still much uncertainty. The attempt has been made to derive them from the Phycomycetes. Not only is the construction of the thallus against this, but the structure of the sexual organs and the development of the fruit in the Ascomycetes indicate on the other hand a connection with the Red Algae. The Uredineae or Rusts, one of the simplest orders of Basidiomycetes, appear to connect the latter group with the Ascomycetes.

The saprophytic or parasitic thallus of the Eumycetes is, like that of the Phycomycetes, composed of fine, richly-branched filaments or hyphae which together form the mycelium (Fig. 66). The hyphae are, however, in this case septate, consisting of rows of cells. The cell membrane, which contains chitin, is usually thin. In the colourless protoplasm there are usually numerous minute nuclei (Fig. 6), while in other cases each cell has a pair of nuclei or only a single nucleus. Chromatophores are wanting and true starch is never formed; the place of the latter is taken by glycogen, often in considerable quantity, and by fat-globules. The hyphae of a mycelium are, as a rule, either isolated or only loosely interwoven; they spread through the substratum in all directions in their search for organic nourishment. In many of the higher Fungi, however, the profusely-branching hyphae form compact masses of tissue. Where the filaments in such cases are in intimate contact and divided into short cells, an apparently parenchymatous tissue or PSEUDO-PARENCHYMA is produced. Such compact masses of hyphal tissue are formed by some species of Fungi when their mycelia, in passing into a vegetative resting stage, become converted into SCLEROTIA, tuberous or strand-like, firm, pseudo-parenchymatous bodies, which germinate under certain conditions (Fig. 36). In the fructifications the hyphae are also nearly always aggregated into a more or less compact tissue (Fig. 37).

The two sub-classes are distinguished by their respective methods of asexual spore-formation. The ASCUS is characteristic of all Ascomycetes; it is a club-shaped sporangium within which a definite number of spores (usually 8) is formed in a peculiar way by free cell formation (Fig. 381). The Basidiomycetes have in place of the ascus a BASIDIUM of varying shape. It may either be four-celled or a unicellular tubular structure from which the spores are abstricted by a process of budding in definite numbers, usually four (Figs. 398, 403, 410).

Sub-Class I.—Ascomycetes (1, 51, 52, 61-74)

The Ascomycetes in their typical forms possess sexual organs, the oogonia, which here go by the name of ascogonia or, as in the Red Algae, of carpogonia, and antheridia. The sexual organs have

been accurately investigated in relatively few forms; a number of distinct types are found.

1. In the Laboulbeniaceae (Fig. 396) the carpogonium with its trichogyne, and the antheridia which produce spermatia, show a striking correspondence with the structures of the same name in the Red Algae.

2. The Ascomycetes which enter into the composition of Lichens (Figs. 429, 430) approach most closely the preceding group. The carpogonium is here a spirally-wound filament of cells terminating in a trichogyne. The spermatia are formed in special flask-shaped depressions of the thallus, the spermogonia. Similar reproductive organs occur in some Ascomycetes which do not form parts of Lichens.

3. *Pyronema* ([69]) (Fig. 390) and related genera, *Ascodesmis* (= *Boudiera* CLAUSSEN) ([69]), *Monascus* ([63]), *Aspergillus* ([66]), exhibit a distinct type. A multinucleate carpogonium which is provided with a trichogyne is fertilised by a multinucleate antheridium, the two structures being thus coenogametes (p. 429). *Lachnea* ([64]) may also be placed here.

4. In the Erysibaceae (Fig. 382) a uninucleate antheridium unites directly with a uninucleate oogonium.

Other genera exhibit transitions in the structure of the carpogonia and antheridia from the type of the Lichen fungi to those of *Pyronema*, and of the Erysibaceae. Thus the former may perhaps be regarded as primitive Ascomycetes and the latter as reduced ([62]).

In some Ascomycetes the sexual organs are present, but no fertilisation of the carpogonium takes place, and in others they are more or less completely reduced.

The carpogonium does not give rise to a resting oospore, but remains in connection with the parent plant; from it ascogenous hyphae or cell-filaments grow out, branch, and ultimately form the asci at the ends of branches. The ascogenous hyphae and asci proceeding from a carpogonium, or in some cases from a group of carpogonia, form a fruit-body or fructification. In the formation of this, vegetative hyphae, derived from the mycelium of the parent plant, and sharply distinct from the ascogenous hyphae, take part. The sterile hyphae grow between and invest the ascogenous filaments. The mycelium which produces the sexual organs represents the sexual generation (gametophyte); the system of hyphae proceeding from the carpogonium and ending in the asci corresponds to the asexual generation (sporophyte).

Within or on the surface of the fructifications of some groups of the Ascomycetes the asci stand parallel to one another in a layer called the hymenium, and between them as a rule are paraphyses borne on the sterile system of hyphae of the fructification.

In some orders of Ascomycetes the sexual organs and the

fructifications are completely wanting, probably owing to reduction. The asci then arise directly from the mycelium.

The ASCUS originates from a single cell; this to start with contains two nuclei, which fuse, and the resulting nucleus by repeated division gives rise to eight nuclei. By a process of free cell formation the spores become limited by cell walls in the way shown in Fig. 21 (Figs. 381, 391). In contrast to the formation of spores in the sporangia of Phycomycetes the cytoplasm of the ascus is not completely used up in the formation of the ascospores. The spores usually form a longitudinal row, embedded in the remaining epiplasm, which contains glycogen, and are ultimately ejected from the ruptured apex of the ascus by the swelling of this. The spores are adapted for dispersal in the air.

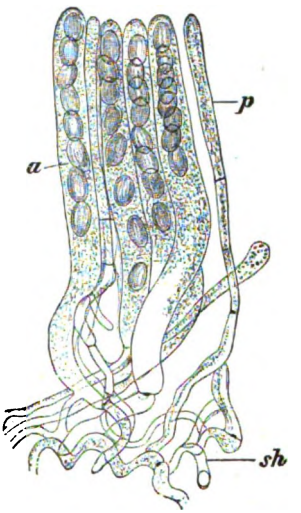


FIG. 381.—Portion of the hymenium of *Morchella esculenta*. *a*, Asci; *p*, paraphyses; *sh*, subhymenial tissue. (× 240. After STRASBURGER.)

In a few cases the eight nuclei before the delimitation of the cells undergo further divisions; numerous free ascospores, *e.g.* 32 in *Thecotheus*, thus arise. More commonly divisions occur after the spores are delimited, and result in the formation of eight bi- or multicellular bodies.

The behaviour of the sexual nuclei in and after fertilisation of the carpogonium is only accurately known in a few cases. For some Ascomycetes (*Pyronema* and *Monascus*) it has recently been shown that the sexual nuclei do not fuse in the carpogonium, but lay themselves side by side. In the ascogenous hyphae the pairs of nuclei divide conjugately, and only in the young ascus do two nuclei, the descendants respectively of a male and a female sexual nucleus, fuse together. Thus the conjugation of the sexual nuclei is here delayed from the carpogonium to the development of the ascus.

So far as the results yet obtained allow of a conclusion being drawn, the reduction division in the Ascomycetes happens, just after the fusion of the two nuclei in the ascus.

In the life-history of the Ascomycetes an asexual reproduction by means of conidia often precedes the development of the fructification. The conidia are spores provided with a cell wall which are budded off from the tips of simple or branched hyphae, the conidiophores (Fig. 384).

According to the construction of the fructification we may distinguish in the first place the orders of the Erysibaceae, Plectascineae, and Pyrenomycetineae, with closed or vase-shaped fruit-bodies (perithecium), the Discomycetes with an open fructification (apothecium), and the Tuberaceae with a fructification that is at first open but becomes completely closed.

To these orders must be added the Exoasceae, in which the asci arise from cells of the mycelium without the formation of any fructification, and the very simple Saccharomycetes or Yeast Fungi. These two groups can be regarded as reduced Ascomycetes.

The Laboulbeniaceae in which the asci are enclosed in small perithecia occupy an isolated position.

The genetic connections of these orders are not yet clearly established.

Order 1. Erysibaceae (Mildew Fungi) [51, 65]

The small spherical perithecia have a closed investment (peridium) which ultimately opens irregularly and liberates the ascospores. The asci stand singly or in a group in the centre of the fruit.

The Erysibaceae live as epiphytic parasites whose mycelium, somewhat

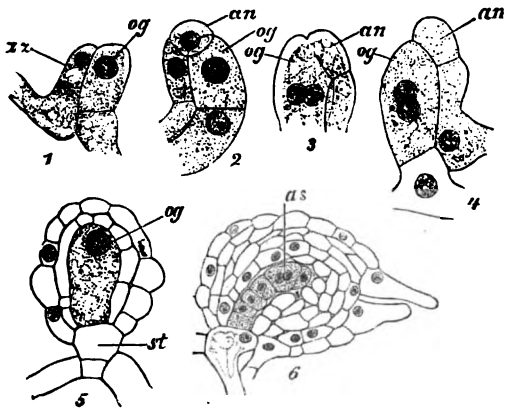


FIG. 382. — *Sphaerotheca castagnei*. Fertilisation and development of the perithecium. *1*, Oogonium (*og*) with the antheridial branch (*as*) applied to its surface; *2*, separation of antheridium (*an*); *3*, passage of the antheridial nucleus towards that of the oogonium; *4*, fertilised oogonium, in *5* surrounded by two layers of hyphae derived from the stalk cell (*st*); *6*, the multicellular ascogonium derived by division from the oogonium; the penultimate cell with the two nuclei (*as*) gives rise to the ascus. (After HARPER.)

resembling a cobweb, and ramifying in all directions over the surface, particularly the leaves, of higher plants, sends out haustoria which penetrate the epidermis of the host. In some cases the mycelium also inhabits the intercellular spaces of the leaf. The ripe ascus fructifications (perithecia) are small black bodies provided with peculiar appendages. In the simplest forms (*e.g.* in the genus *Sphaerotheca*) the spheroid perithecium encloses only a single ascus with eight spores. It is enveloped by a covering of sterile hyphae, forming a sheathing layer, two to three cells deep. The genera *Erysibe* and *Uncinula*, on the other hand, develop several asci in each perithecium, and in *Phyllactinia* 12 to 25 asci are present. Since all the eight nuclei are not utilised in spore formation the number of spores in each ascus is usually 4, or only 2. The perithecia are irregularly ruptured at their apices and the spores are thus set free. As HARPER has shown, the first rudiment of the perithecium consists of an oogonium and

an antheridium. These are uninucleate cells, separated from the mycelium by partition walls, and stand close together. The male nucleus passes into the oogonium by an opening which forms in the cell walls (Fig. 382, 1-4). After fertilisation the oogonium is surrounded by investing filaments which spring from its stalk cell or from that of the antheridium (5), and the oogonium itself becomes converted into a multicellular structure (6). In *Sphaerotheca* the ascus containing eight spores arises from the binucleate penultimate cell, while in *Erysibe* and *Phyllactinia* this cell exclusively or mainly produces ascogenous hyphae which in turn give rise to the numerous asci. Before entering upon the formation of perithecia, the Mildew Fungi multiply by means of conidia abstricted in chains from special, erect hyphae, from the tip downwards. These are distributed by the wind. The Mildew Fungus occurs on the leaves and berries of *Vitis* in America and has appeared in Europe on the Grape-vine since 1845. This fungus, known as *Oidium Tuckeri*, is the conidial form of *Uncinula necator* (= *U. spiralis*), the small perithecia of which have appendages spirally rolled at their free ends and are only rarely found (Fig. 383).

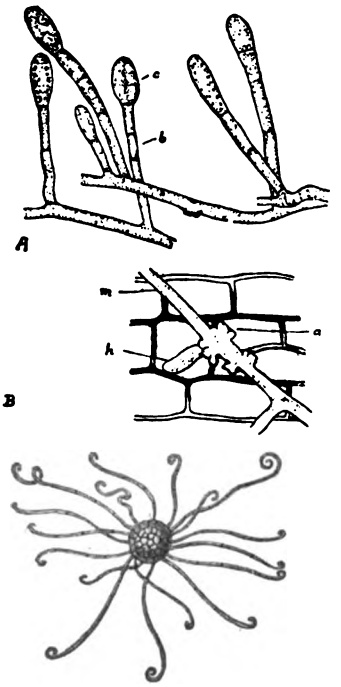


FIG. 383.—*Uncinula necator*. *A*, Conidial stage; *c*, conidium; *b*, conidiophore. *B*, Hypha which has formed a disc of attachment (*a*) and has sent a haustorium (*h*) into an epidermal cell. *C*, Perithecium with appendages. (From SORAUER, LINDAU, and REH. *Handb. d. Pflanzenkrankheiten*, ii. p. 194. 1906.)

Order 2. Plectascineae

The spherical perithecia have a closed peridium; the asci are irregularly arranged within this.

1. **Aspergillaceae** (66). Fructification small; not subterranean. Here belong two of the most common Mould Fungi, *Aspergillus* (*Eurotium*) *herbariorum* and *Penicillium crustaceum*, which live saprophytically on organic substances. Both multiply extensively by means of conidia before they begin to form perithecia.

In the case of *Aspergillus herbariorum*, the conidia are abstricted in chains from a number of sterigmata arranged radially on the spherical, swollen ends of the conidiophores (Fig. 384). The conidiophores are closely crowded together, and constitute a white mould, afterwards turning to a blue-green, frequently found on damp vegetables, fruit, bread, etc. Some species of *Aspergillus* are pathogenic in man and other mammals; thus *A. fumigatus*, which lives in fermenting heaps of hay at an optimum temperature of 40° C. (67), causes mycosis of the external ear, the throat, and the lungs.

In *Penicillium crustaceum*, another widespread blue-green mould, the erect conidiophores (Fig. 384) are verticillately branched. The spherical perithecia of *Aspergillus* and *Penicillium* are produced later on the mycelium, but only rarely occur in the latter genus. They develop from the sexual organs consisting of

an antheridium and a carpogonium provided with a trichogyne. The walls of the asci and the surrounding pseudo-parenchyma disappear in the ripe fructification which opens irregularly by the rupture of the peripheral layer.

2. The **Elaphomycetaceae** have subterranean, truffle-like fructifications, the peridium of which is sharply marked off from the powdery mass of spores derived from the ascogenous hyphae. *Elaphomyces granulatus* (*Boletus cervinus*), the yellowish-brown fructifications of which are of the size of a walnut and have a bitter taste, occurs commonly in woods in Europe. It is used in veterinary medicine.

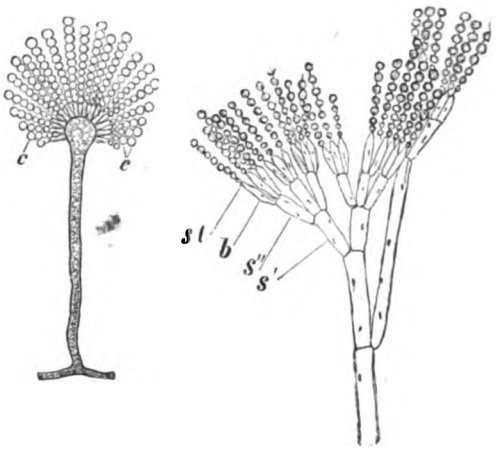


FIG. 384.—Conidiophores of *Aspergillus herbariorum* (to the left) and *Penicillium crustaceum* (to the right).

3. The **Terfeziaceae** are distinguished from the preceding group by the peridium of the fructification not forming a sharply distinct layer. Species of *Terfezia* with edible truffle-like fructifications occur in the Mediterranean region.

Order 3. Pyrenomycetes

The Pyrenomycetes comprise an exceedingly varied group of Fungi, some of which are parasitic upon different portions of plants, and others are saprophytic upon decaying wood, dung, etc., while a few genera occur as parasites upon the larvae of insects. The flask-shaped fructifications or perithecia are characteristic of this order. The perithecia are open at the top, and are covered inside, at the base, with a hymenial layer of asci and hair-like paraphyses (Fig. 385). The lateral walls are coated with similar hyphal hairs, the periphyses. The ascospores escape from the perithecia through the aperture.

The simplest Pyrenomycetes possess free perithecia (Fig. 385) which are usually small and of a dark colour, and grow singly on the inconspicuous mycelium (*e.g. Nectria*, *Sphaeria*, and *Podospora*). In other cases the perithecia are in groups embedded in a cushion- or club-shaped, sometimes branching, mass of compact mycelial hyphae having a pseudo-parenchymatous structure. Such a fructification is known as a STROMA.

In the life-history of most Pyrenomycetes the formation of perithecia is pre-

ceded by the production of various accessory fructifications, particularly of conidia, which are abstricted in different ways, either directly from the hyphae or from special conidiophores, and assist in disseminating the fungus. The conidiophores are frequently united in distinct, conidial fructifications. A special form of such fructifications are the PYCNIDIA produced by many genera. They are small spherical or flask-shaped bodies which give rise to branched hyphal filaments from the apices of which conidia, in this case termed PYCNOSPORES or PYCNOCONIDIA, are abstricted (Fig. 386). The structure of the pycnidia and pycnospores corresponds to that of the spermogonia and spermatia of the Lichens, and they may be regarded as the original male organs.

Claviceps purpurea, the fungus of Ergot, is important on account of its official value. It is parasitic in the young ovaries of different members of the Gramineae, particularly of Rye. The ovaries are infected in early summer by the ascospores. The mycelium soon begins to form conidia, which are abstricted in small clusters from short lateral conidiophores (Fig. 387 *A*).

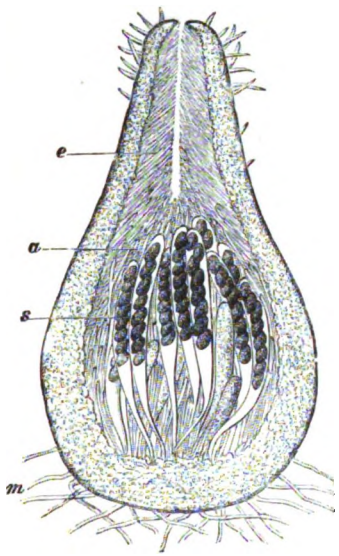


FIG. 385.—Perithecium of *Podospora fimiseda* in longitudinal section. *s*, Asci; *a*, paraphyses; *e*, periphyses; *m*, mycelial hyphae. (× 90. After v. TAVEL.)

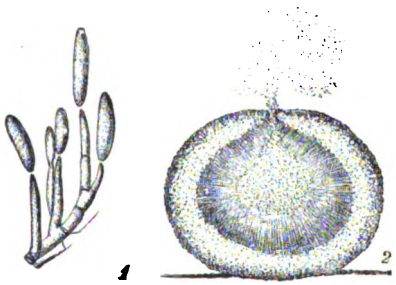


FIG. 386.—*1*, Conidiophore abstricting conidia, from a pycnidium of *Cryptospora hypodermia*. (× 300. After BREFELD.) *2*, Pycnidium of *Strickeria obducens* in vertical section. (× 70. After TULASNE.)

At the same time a sweet fluid is extruded. This so-called HONEY-DEW is eagerly sought by insects, and the conidia embedded in it are thus carried to the ovaries of other plants. After the completion of this form of fructification, and the absorption of the tissue of the ovary by the mycelium, a sclerotium is eventually formed in the place of the ovary from the hyphae of the mycelium by their intimate union, especially at the periphery, into a compact mass of pseudo-parenchyma (Fig. 36). These elongated dark-violet SCLEROTIA, which project in the form of slightly curved bodies from the ears of corn, are known as Ergot, SECALE CORNUTUM (Fig. 387 *B*). The sclerotia, copiously supplied with reserve material (fat), eventually fall to the ground, where they pass the winter, and germinate in the following spring when the Rye is again in flower. They give rise to bundles of hyphae which produce long-stalked, rose-coloured globular heads (*C*). Over the surface of the latter, numerous sunken perithecia (*D*, *E*) are distributed. Each perithecium contains a number of asci with eight long, filiform ascospores, which are ejected and carried by the wind to the inflorescences of the grass.

Nectria ditissima (68) is a very injurious parasitic fungus which inhabits the

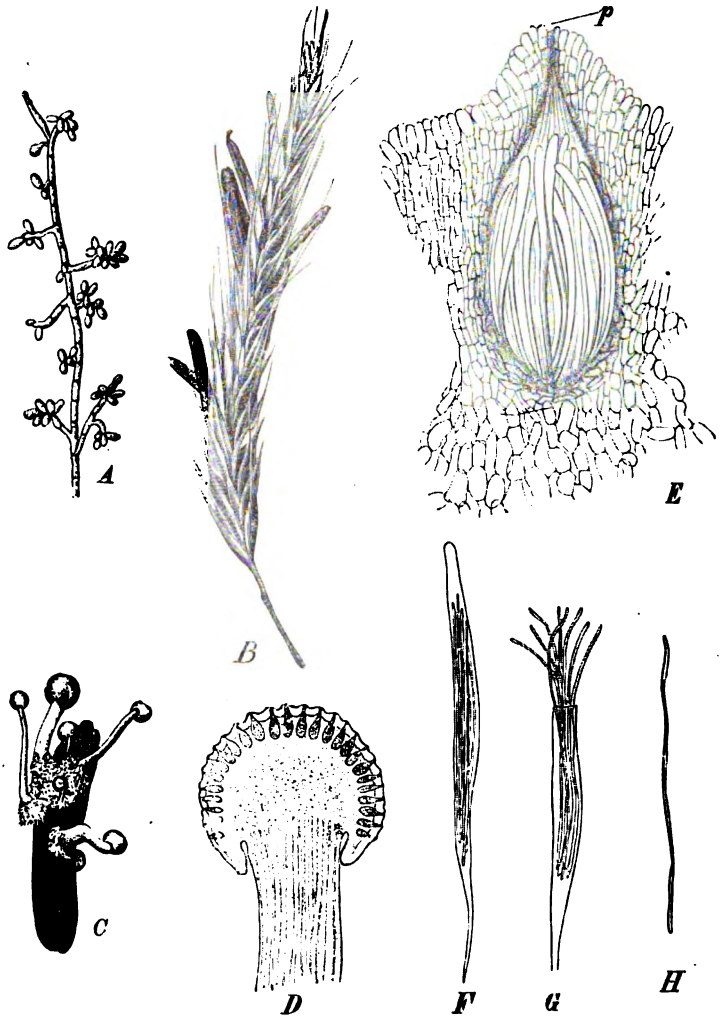


FIG. 387.—*Claviceps purpurea*. *A*, Mycelial hypha with conidia; *B*, ear of Rye with several ripe sclerotia; *C*, a sclerotium with stromata; *D*, longitudinal section of a fructification showing numerous perithecia; *E*, a single perithecium, more highly magnified; *F*, ascus with eight filiform spores; *G*, a ruptured ascus with escaping spores; *H*, a single spore. (*A* after BREFELD; *C-H* after TULASNE; *B* photographed from nature. *OFFICIAL* and *POISONOUS*.)

cortex of various trees and causes the canker of fruit trees. It forms in winter and spring small red perithecia which are closely crowded together.

OFFICIAL.—Ergot is the sclerotium of *Claviceps purpurea*.

Order 4. Discomycetes (60)

The Discomycetes are distinguished from the other orders by their open apothecia, which bear the hymenium, consisting of asci and paraphyses, freely exposed on their upper surface (Figs. 381, 389). The different groups exhibit great diversity as regards the manner of development of their fructifications.

The great majority of the Discomycetes, of which the genus *Peziza* may serve as a type, grow on living or dead vegetable substances, especially upon decaying wood, but sometimes also on humus soil. They produce saucer- or cup-shaped fructifications of a fleshy or leathery consistency, and usually of small dimensions. One of the largest forms, *Peziza aurantiaca* (Fig. 388), has irregularly bowl-shaped fructifications, which may be seven centimetres broad and of a bright orange-red colour, while in most of the other species they are grey or brown. Such cup-shaped fructifications are termed APOTHECIA.

FIG. 388.—*Peziza aurantiaca.* (Nat. size. After KROMBHOLZ.)

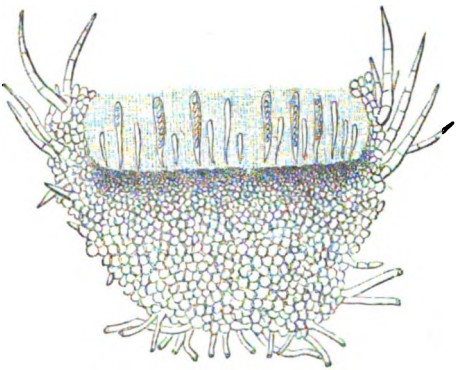


FIG. 389.—*Lachnea pulcherrima.* Apothecium ruptured, showing old and young asci between the paraphyses. (After WORONIN, from v. TAVEL.)

The development of the apothecium may be described for *Pyronema confluens*, in which it was first thoroughly investigated by R. HARPER. The fruit-body of this species is about 1 mm. across, and of a yellow or reddish colour; it often occurs on spots where fires have been kindled in woods. The carpogonia are especially large in this species, and several usually take part in the formation of each apothecium (Fig. 390 *A*). The carpogonium or ascogonium consists of the spherical, multinucleate oogonium, on the apex of which a multinucleate curved cell, the trichogyne, is situated. The cylindrical, multinucleate antheridium arises from a neighbouring hypha; its apex comes into open communication with the tip of the trichogyne by the breaking down of the intervening walls. The male nuclei first wander into the trichogyne cell, and then, by the breaking down of the basal wall of the latter, into the oogonium. The egg-cell then becomes limited from the trichogyne by a new cell wall and sends out ascogenous filaments containing the conjugate nuclei. These filaments branch and ultimately terminate in asci (*E*), while the sterile hyphae and the paraphyses of the fructification are derived from hyphae arising beneath the carpogonium. According to HARPER the male and female nuclei fuse in pairs with one another in the carpogonium. More recent investigations by CLAUSSEN show that they only place

themselves side by side, and in the ascogenous hyphae divide conjugately, but remain distinct from one another. The fusion of a descendant of a male nucleus

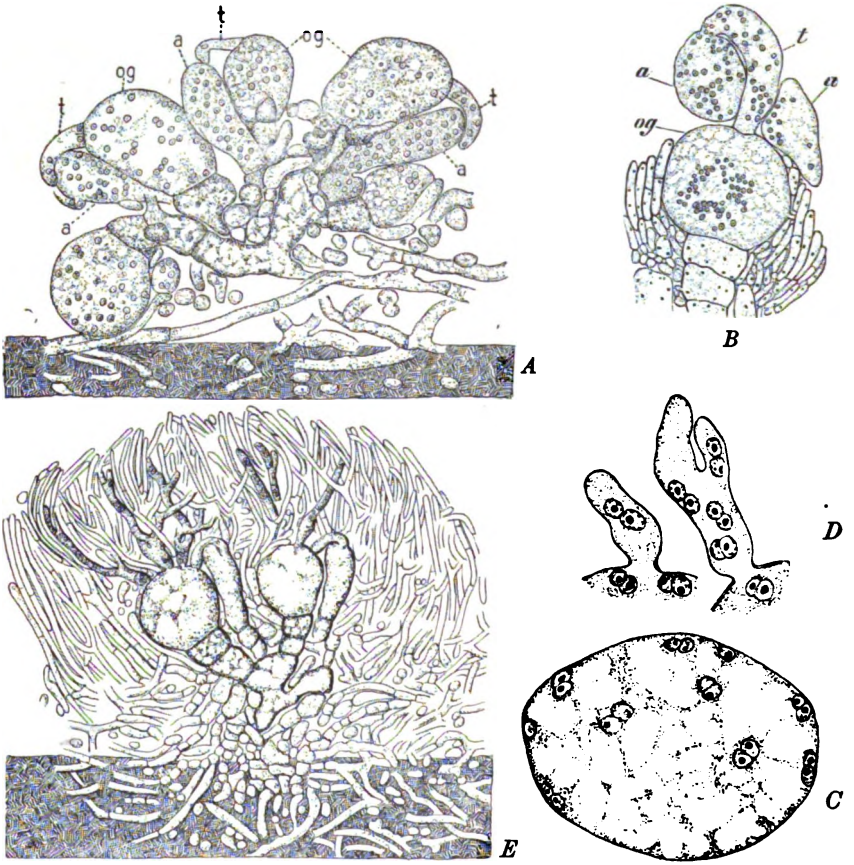


FIG. 390.—*Pyronema confluens*. *A*, Very young apothecium; *og*, oogonia, with trichogynes (*t*); *a*, antheridia (× 450). *B*, Fusion of the antheridium with the tip of the trichogyne (× 800). *C*, The association in pairs of the male and female nuclei in the oogonium, which is cut transversely (× 1000). *D*, Passage of the paired nuclei into the ascogenous hyphae (× 1000). *E*, Young apothecium. The ascogenous hyphae springing from the oogonia have branched and are invested by sterile hyphae (× 450). (*B* after HARPER. *A*, *C*, *D*, *E* after CLAUSSEN.)

with the descendant of a female nucleus does not take place till the development of the ascus (Fig. 391).

In many Discomycetes a reduction of the sexual organs has taken place associated with a loss of sexuality. The antheridia are functionless or completely suppressed, and in extreme cases the ascogonia are also wanting, only a tangle of hyphae being recognisable in their position. The ascogenous hyphae in the young fructification are, however, always present.

The asci develop in various ways at the ends of ascogenous hyphae. As a rule

the end of the ascogenous hypha when about to form an ascus becomes curved into a hook-like shape (Fig. 391 *A*). The two nuclei of the young ascus (*a*) lie near to the bend, and on the formation of transverse walls are separated from the uninucleate terminal cell (*h*) and the stalk-cell (*s*), which also has a single nucleus. The two nuclei of the young ascus fuse (*C*), and the resulting nucleus gives rise by repeated division to the nuclei of the eight ascospores (*D*). The terminal cell of the hook (*h*) and the stalk-cell (*s*) have their cavities continuous, so that a binucleate fusion cell results which can proceed to form another young ascus. In this way complicated systems of ascogenous hyphae arise.

The highest development is exhibited by the peculiar fructifications of the Helvellaceae, the mycelium of which grows in the humus soil of woods. In the

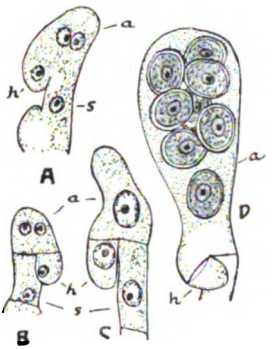


FIG. 391.—Development of the ASCUS. *A-C*, *Pyronema confluens*. (After HARPER.) *D*, Young ascus of *Boudiera* with eight spores. (After CLAUSSEN.) Explanation in text.

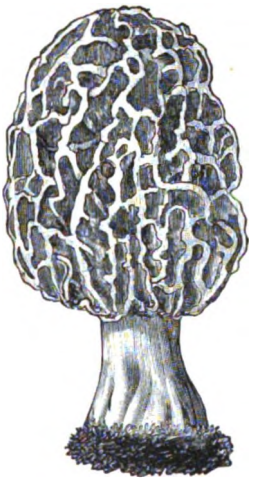


FIG. 392.—*Morchella esculenta*. (½ nat. size.)

genus *Morchella* (Fig. 392) the fructifications consist of a thick erect stalk, bearing a club-shaped or more or less spherical cap or pileus, which bears the hymenium, with the eight-spored asci, on the reticulately-indented exterior surface (Fig. 381). The Morchellas are edible ([70]), in particular *M. esculenta* and *M. conica*. The former has a yellowish-brown cap, ovately spherical in shape, and attains a height of 12 cm.; the cap of the latter is conical and dark brown, and it reaches a height of 20 cm. *Gyromitra esculenta*, with dark brown cap and white stalk, and others are also edible. In their external appearance the fructifications of these highly developed Discomycetes greatly resemble those of the Basidiomycetes.

Order 5. Tuberaceae (Truffles) ([71])

The Tuberaceae or Truffle Fungi are saprophytic Ascomycetes, the mycelium of which occurs in humus soil, particularly in woods. The ascus fructifications familiar under the name of truffles are underground tuberous bodies, consisting of a thick, investing layer, with passages opening to the exterior; the walls of these are lined with the hymenium composed of club-shaped asci (Fig. 393). The asci contain only a small number of spores; in the case of the true Truffles (*Tuber*) they are usually only four in number, and generally have a spinous or reticulately-

thickened epispore. They are set free in the soil by the breaking down of the asci and of the wall of the fructification.

The fructifications of many of the Tuberaceae are edible (70), and have an aromatic odour and taste. They are, for the most part, obtained from France and Italy.

FIG. 393.—*Tuber rufum*. *1*, A fructification in vertical section (× 5); *a*, the cortex; *d*, air-containing tissue; *c*, dark veins of compact hyphae; *h*, ascogenous tissue. *2*, A portion of the hymenium (× 460). (After TULASNE, from v. TAVEL. *Pilze*.)

Of the edible varieties, the most important are the so-called black truffles belonging to the genus *Tuber*, viz. *Tuber brumale, melanosporum* (Perigord Truffle), *aestivum, mesentericum*. The fructifications of these species have a warty cortex of a black, reddish-brown, or dark brown colour. The white truffle, *Choiromyces meandriformis*, the external surface of which is pale brown, is also edible.

The fructifications when very young are open as in the Discomycetes. The Truffles seem most nearly related to the Helvellaceae.

Order 6. Exoasceae [72]

The most important genus of this group of Ascomycetes is *Taphrina* (including *Exoascus*), the species of which are parasitic on various trees. They develop, in part annually, beneath the cuticle of the leaves, causing discolorations of these organs; their mycelium persists during the winter in the tissue of the host, so that a constant recurrence of the disease takes place. The presence of the mycelium in the tissues of the infected part causes the abnormally profuse development of branches known as WITCHES'-BROOMS. *Taphrina Carpini* produces the abnormal growths occurring on the Hornbeam; *Taphrina Cerasi* those on Cherry trees. *Taphrina deformans* attacks the leaves of the Peach and causes them to curl. *Taphrina Pruni* is parasitic in the young ovaries of many species of *Prunus*, and produces the malformation of the fruit known as "Bladder Plums," containing a cavity, the so-called "pocket," in the place of the stone; the mycelium persists through the winter in the branches. In the formation of asci, the copiously-branched mycelium ramifies between the epidermis and cuticle of the infected part. The individual cells of the mycelium become greatly swollen and grow into club-shaped tubes, which burst through the cuticle and, after cutting off a basal stalk-cell, are usually converted into asci with eight spores (Fig. 394). As in other Ascomycetes the young ascus has two nuclei which fuse, and the resulting nucleus undergoes three divisions to give the nuclei of the eight spores. The numerous asci are closely crowded together.

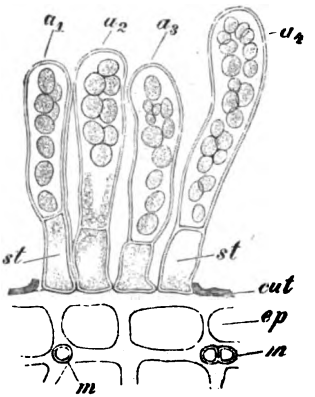


FIG. 394.—*Taphrina Pruni*. Transverse section through the epidermis of an infected plum. Four ripe asci, a_1, a_2 with eight spores, a_3, a_4 with yeast-like conidia abstricted from the spores; *st*, stalk-cells of the asci; *m*, filaments of the mycelium cut transversely; *cut*, cuticle; *ep*, epidermis. (× 600. After SADEBECK.)

The spores, which bud in water or sugar solution, frequently germinate whil still enclosed within the asci (Fig. 394 a_3, a_4), and give rise by budding to yeast-like conidia, *e.g.* in *Taphrina Pruni*.

The Exoasceae are perhaps to be regarded as reduced Ascomycetes, in which the sexual organs have become completely suppressed.

Order 7. Saccharomycetes (Yeast Fungi) [73]

The beer, alcohol, and wine yeasts included in the genus *Saccharomyces* are simple unicellular Fungi which have the form of spherical, oval, or cylindrical cells containing a single nucleus. They increase in number by budding (Fig. 395). No mycelium is formed, though sometimes the cells remain for a time united in chains. With free access of oxygen and at a suitable temperature yeasts form asci when the nutrient substratum is exhausted; the asci externally resemble the yeast-cells, but contain a few spores. In some yeasts a conjugation of two cells accompanied by a nuclear fusion has been observed. In *Saccharomyces Ludwigii* the four spores in the ascus germinate and fuse in pairs by means of a narrow conjugation-tube; the latter elongates into a germ-tube from which yeast-cells are abstricted. In the ginger-beer yeast (*Zygosaccharomyces*) and in *Schizosaccharomyces* the yeast-cells conjugate

by means of long tubes before spore-formation. These nuclear fusions possibly correspond to those in the young asci of other Ascomycetes.

Physiologically these fungi are remarkable for their power of exciting, by means of an enzyme (zymase), the fermentation of saccharine solutions, alcohol and carbon dioxide being produced (cf. p. 274). The beer yeast (*Saccharomyces cerevisiae*) is only known in the cultivated form; the wine yeast (*S. ellipsoideus*), on the other hand, occurs regularly in the soil of vineyards in the spore-form; the latter is therefore always present on the grapes and need not be added to the grape-juice. Other genera, in some of which a mycelium is developed, belong to this order.

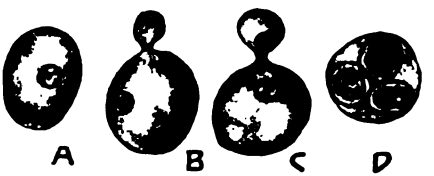


FIG. 395.—*Saccharomyces cerevisiae*. *A*, Yeast-cell; *B*, *C*, yeast-cell budding; *D*, ascus with four spores. (× 1125. After GUILLIERMOND.)

No evidence is at present forthcoming to show that the Yeasts are to be regarded as developmental forms of other fungi. In various members of the Exoasci and Ustilagineae, however, yeast-like conidia which reproduce by budding are known. Possibly the Saccharomycetes are reduced Ascomycetes, or they may represent an independent group of very simple fungi at the base of the Ascomycetes.

Owing to their richness in readily digestible substances, especially proteids and glycogen, but also fats, yeast has a considerable food-value. It is purified, dried at 125° C., and sold for this purpose.

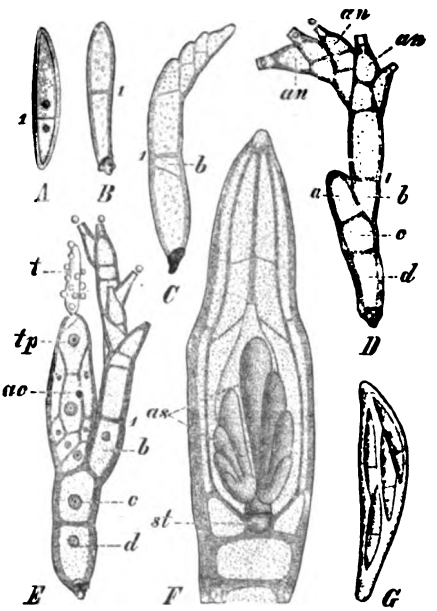


FIG. 396.—*Stigmatomyces Baerii*. Description in text. *A*, Spore. *B-F*, Successive developmental stages. *D*. With spermatia escaping from the antheridia *an*. *E*. With antheridia above and the lateral female organ, *F*, Perithecium with developing asci. *G*, Ripe ascus (After THAXTER.)

Order 8. Laboulbeniaceae (74)

The Laboulbeniaceae are a group of minute fungi occupying an isolated position; our knowledge of them is largely due to the work of THAXTER. Their thallus consists of two to a number of cells, and is attached to the body of the insect, most commonly a beetle, on which it is parasitic by means of a pointed process of the lowest cell inserted into the chitinous integument of the insect, or by means of rhizoids which penetrate more deeply. *Stigmatomyces Baerii* which occurs on house-flies in Europe may be taken as an example. The bicellular spore (Fig. 396 *A*), which has a mucilaginous outer coat, becomes attached by its lower end (*B*), and divisions occur in both cells (*C*). From

the upper cell an appendage is developed bearing a number of unicellular, flask-shaped antheridia (*D*, *an*) from which naked spherical spermatia without cilia are shed. The lower cell divides into four (*D*, *a*, *b*, *c*, *d*), and the cell *a* projects and gives rise to the multicellular female organ. The true egg-cell (*E*, *ac*), which is called the carpogonium, is surrounded by a layer of cells. Above the carpogonium come two cells (*E*, *tp*, *t*), the upper of which is the freely-projecting trichogyne or receptive organ for the spermatia. After fertilisation the carpogonium becomes divided into three cells, of which the uppermost disappears, the lowest (*F*, *st*) remains sterile, while from the middle cell the asci grow out. Each ascus (*G*) produces four spindle-shaped, bicellular spores. The sexual nuclei become associated in a pair in the carpogonium and divide conjugately. The nuclear fusion only takes place in the young ascus. In certain species in which antheridia are wanting a second nucleus, according to FAULL, is derived from the stalk-cell of the trichogyne.

Sub-Class II.—Basidiomycetes (1, 51, 52, 75-86)

The Basidiomycetes no longer possess sexual organs; only in the Uredineae or Rust Fungi are structures found which can be regarded as persisting, though functionless, male organs, and cells which appear to correspond to the carpogonia of Ascomycetes. In place of asci, BASIDIA are present which produce by a process of budding in most cases four BASIDIOSPORES. The basidia agree with the asci in containing when young two nuclei, which fuse with one another. The reduction division appears to follow on this nuclear fusion or karyogamy. The resulting nucleus undergoes two divisions, and the four resulting nuclei pass into the spores which are budded off (Fig. 397).

The alternation of generations present in the Ascomycetes can no longer be demonstrated in the Basidiomycetes (with the exception of the Uredineae) owing to the absence of the sexual organs. The union of sexual cells is replaced by cell-fusions that result in binucleate cells. The pairs of nuclei correspond to diploid nuclei, but fusion of the two haploid nuclei of the pair only takes place in the young basidium. On the division of the truly diploid nucleus thus produced, haploid nuclei again arise.

The basidia present three distinct types. In the orders Uredineae and Auricularieae the upper portion of the basidium is divided by transverse walls into four cells; each cell bears a single spore on a thin stalk (sterigma), arising near the upper end (Figs. 403, 408). In the Tremellineae, on the other hand, the basidium is divided by longitudinal walls into four cells, each of which continues into a long tubular sterigma (Fig. 398). The basidium in the Exobasidiineae, Hymenomycetes, and Gasteromycetes is unicellular, and bears as a rule four spores at the summit; these may be sessile or situated on sterigmata (Figs. 397; 420, 2). The Ustilagineae are of interest, since in one family of these fungi the basidia are divided, while in the other they are undivided; the number of spores produced is not a definite one, but often very large.

In addition to basidia, the Basidiomycetes, like the Ascomycetes, produce various forms of conidia as accessory fructifications in many species. The origin of asexual spores by hyphal cells rounding off and developing a thick wall and their ultimate separation is different from that of conidia (chlamydospores

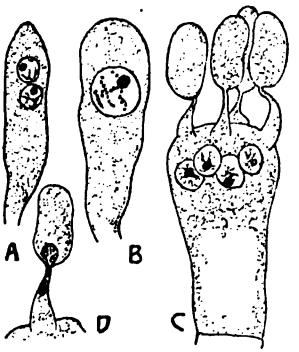


FIG. 397.—*Armillaria mellea*. *A*, Young basidium with the two primary nuclei; *B*, after fusion of the two nuclei. *Hypholoma appendiculatum*, *C*, a basidium before the four nuclei derived from the secondary nucleus of the basidium have passed into the four basidiospores. *D*, Passage of a nucleus through the sterigma into the basidiospore. (After RUHLAND.)

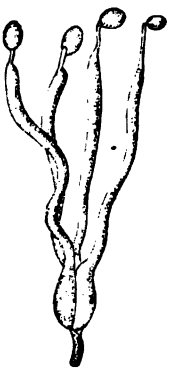


FIG. 398. — Basidium of one of the Tremellineae (*Tremella lutescens*) (after BREFELD). (× 450. From v. TAVEL, *Pilze*.)

according to BREFELD). These appear in the Ustilagineae as the smut-spores, and as the rust-spores in the Uredineae. In the former the basidia arise directly from spores of this kind (Fig. 400), in the latter from a definite type of rust-spore (Fig. 403, 2). In other Basidiomycetes, if a few simple forms are disregarded, the basidia are always borne upon or within more or less complicated fructifications. The layer in which the basidia are associated together is termed the hymenium. These fructifications correspond to those of the Ascomycetes, but no sexual organs are concerned in their origin. The young basidia, corresponding to the smut- and rust-spores, here arise from hyphae of the fructification without the formation of chlamydospores.

Order 1. Ustilagineae (Smut Fungi) [76]

The Ustilagineae are parasites, and their mycelium is found ramifying in higher plants, usually in definite organs, either in the leaves and stems, or in the fruit or stamens. The Gramineae in particular serve as host plants; certain species of Ustilagineae are in a high degree injurious to cereals, and produce in the inflorescences of Oats, Barley, Wheat, Millet, and Maize the disease known as Smut.

The mycelium ultimately produces resting-spores by the formation of additional transverse walls, and by the division of its profusely-branched hyphae into short swollen cells. The cells become rounded off and converted into spores within a gelatinous envelope, which, however, eventually disappears. The spores then become invested with a new, thick wall. In this way the mycelium is

transformed into a dark brown or black mass of spores. These smut-spores, brand-spores, or resting-spores are scattered by the wind, and germinate only after an interval of rest, producing the basidia in the succeeding spring; the formation of these is characteristically different in the two families of the Ustilaginaceae and the Tilletiaceae.

The most important genus of the **Ustilaginaceae** is *Ustilago*. *Ust. Avenae*, *U. Hordei*, and *U. Tritici segetum*, which were formerly united as *U. Carbo*, cause the "smut" or "brand" of Oats, Barley, and Wheat. The mycelium penetrates the ovary, and forms dark brown, dust-like masses of escaping resting-spores. *U. Maydis* produces on the stalks, leaves, and inflorescences of the Maize tumour-like swellings filled with brand-spores in the form of a black powder. Other

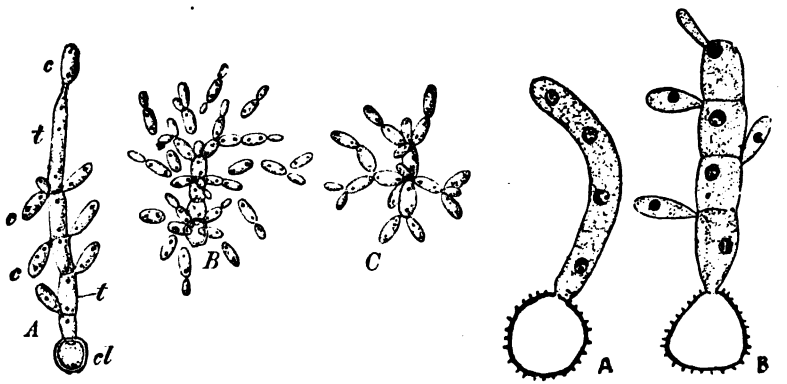


FIG. 399.—*Ustilago*. *A*, Germinating smut-spore (*cl*), cultivated in nutrient solution; *t*, transversely septate basidium with lateral and terminal basidiospores (conidia) (*c*) (× 450). *B*, Germinating conidia, which are multiplying by budding (× 200). *C*, An aggregation of budding conidia (× 350). (After BREFELD, from v. TAVEL, *Pilze*.)

FIG. 400.—*Ustilago Scabiosae*. *A*, Young basidium with four nuclei formed on germination of the resting spore. *B*, Spore-formation on the 4-celled basidium. (After HARPER.)

species live on the leaves of different grasses; while *U. antherarum* occurs in the anthers of various Caryophyllaceae (*e.g. Lychnis*, *Saponaria*). In the case of female flowers of *Lychnis* the presence of the fungus causes the development of stamens, the anthers of which are filled with brand-spores.

The brand-spores of *Ustilago* fall to the ground, and after a period of rest give rise, on germinating, to a short tube (promycelium) which becomes divided by three or four transverse walls (Fig. 400 *B*), and, functioning as a basidium, produces ovate basidiospores (sporidia), both laterally from the upper ends of the intermediate cells and also from the tip of the terminal cell. When abundantly supplied with nourishment, as when cultivated in a nutrient solution, conidia are continuously abstricted in large numbers (Fig. 399), and then multiply further by budding. If the supply of nutriment in the substratum is insufficient, fusions between conidia or between cells of the promycelium take place in many Smut Fungi (Fig. 402). After the food-supply of the substratum is exhausted, the conidia grow out into mycelial hyphae. The formation of the conidia in the damp manured soil of the grain fields is accomplished during a saprophytic mode of existence, but the hyphal filaments which are eventually produced become parasitic, and penetrate the young seedlings as far as the apical cone where the inflorescence takes its

origin. The mycelium continues its development in the inflorescence, and ultimately terminates its existence by the production of brand-spores.

In addition to the infection of young plants, either resting-spores or the conidia resulting from their germination may be carried to the stigmas of the grass-flowers and germinating there produce a mycelium which penetrates to the young seeds and passes the winter in the embryo-plants. Such infection of the flowers may alone take place as in *Ustilago Tritici*, *U. Hordei*, and *U. antherarum*, or the seedling may more often be infected as in *U. Avenae*, *U. Sorghi*, *U. Panici miliacei*, *U. Crameri*. The Smut of Maize can infect all parts of the plant while in a young state and the disease is limited to the infected spots.

The life-history of the **Tilletiaceae** is similar to that of the Ustilaginaceae. The best-known species are *Tilletia Tritici* (= *T. Caries*) and *Tilletia laevis*, the fungi of the stink-brand of wheat. The resting-spores fill the apparently healthy grains and smell like decayed fish. In the first-named species the resting-spores are reticulately thickened ; those of *T. laevis*, on the other hand, are smooth-walled.

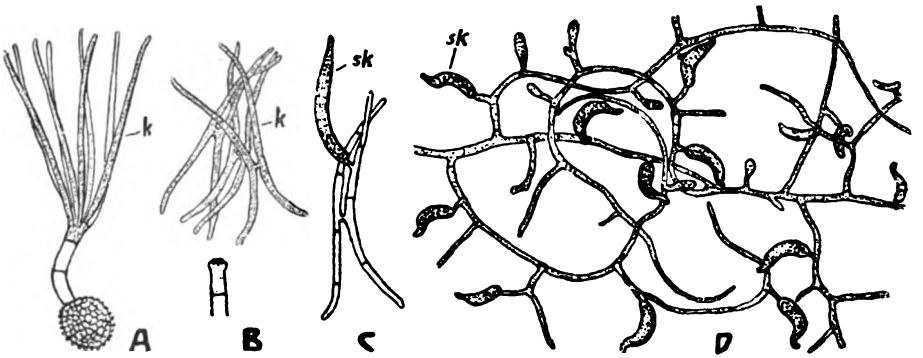


FIG. 401.—*Tilletia Tritici*. *A*, The basidium developed from the brand-spore bearing at the end four pairs of spores *k* (× 300). *B*, The dispersion of the spores which have fused in pairs (× 250). *C*, One of the paired spores germinating and bearing a sickle-shaped conidium *sk* (× 400). *D*, Mycelium with sickle-shaped conidia (× 350). (After BREFELD.)

Unlike the Ustilaginaceae, the germ-tube gives rise only at its apex to filiform basidiospores, which are disposed in a whorl, and consist of four to twelve spores (Fig. 401 *A*). The basidiospores also exhibit the peculiarity that they coalesce with one another in pairs in an H-form. The filiform spores germinate readily, and produce sickle-shaped conidia at the apex of the germ-tubes (Fig. 401 *C*). When abundantly supplied with food material, the germ-tubes grow into large mycelia, from which such sickle-shaped conidia are so abundantly abstricted that they have the appearance of a growth of mould (*D*). Thus *Tilletia*, unlike *Ustilago*, produces conidia of two forms; but in other particulars the development of both groups is the same.

As regards the behaviour of the nuclei, in the Ustilagineae the young spore as a rule has two nuclei which then fuse. In the germination of the spore a reduction division may therefore be anticipated. The cells of the promycelium and the sporidia are uninucleate and mark the commencement of the haploid phase. The binucleate condition is again attained in various ways. In *U. Maydis* the parasitic mycelium consists of uninucleate cells until, shortly before the formation of spores, neighbouring cells of the hypha fuse and thus the binucleate

cells which form the spores arise. On the other hand, *U. Carbo* and the majority of the Ustilagineae attain the binucleate condition by a process of fusion between pro-mycelial cells, sporidia, or the cells of the mycelium arising from these (Fig. 402). This also holds for *Tilletia* in which the sporidia before they are shed are united in pairs, the nucleus from one sporidium passing into the other. The hyphal cells and secondary sporidia and the cells of the parasitic mycelium are therefore binucleate.

In the various Ustilagineae the haploid and diploid phases do not exactly correspond.

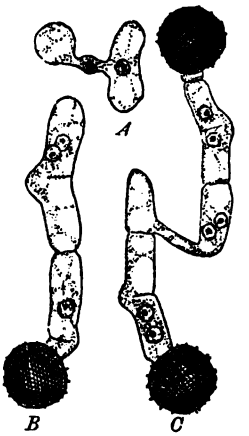


FIG. 402.—*Ustilago Carbo*. *A*, Conjugating sporidia. *B*, The two uppermost cells of a promycelium fusing to give rise to a binucleate cell. *C*, Conjugation between two promycelia. (× 1000. After RAWITSCHER.)

Order 2. Uredineae (Rust Fungi) (77, 78)

The mycelium of the Uredineae lives parasitically in the intercellular spaces of the tissues of the higher plants, especially in the leaves, and gives rise to the widely-spread diseases known as Rusts. Their more varied spore-formation is a distinguishing feature as contrasted with the Ustilagineae.

As in the latter order, the basidia are not produced directly on the mycelium but on the germination of a special type of spore, TELEUTOSPORES or winter spores, which are characteristic of all Uredineae. The teleutospores arise in small clusters beneath the epidermis of the diseased leaf from the ends of hyphae; frequently two or more form a short chain. They are thick-walled resting-spores and persist through the winter (Fig. 403, 1, 5 *t*). The group of spores usually bursts through the epidermis. At first the spores, like the cells of the mycelium which bears them, have two nuclei, but the nuclei fuse before the spore is ripe.

In the germination of the teleutospore a BASIDIUM (promycelium) grows from each cell (Fig. 403, 2); it becomes divided by transverse septa into a row of four cells from each of which a sterigma bearing a single uninucleated BASIDIOSPORE (sporidium) is produced. The sporidia are dispersed by the wind and germinate in the spring on the leaves of host plants (which may be of the same or different species from the one on which the teleutospores were produced), giving rise to an intercellular mycelium, all the cells of which are uninucleate. From this mycelium organs of two kinds arise, spermogonia on the upper surface of the leaf and aecidia on the lower surface.

The SPERMOGONIA (Fig. 404) are flask-shaped structures, the base of which is covered with the projecting ends of hyphae; from these are abstricted spermatia, each of which has a single nucleus. Morphologically they are completely comparable to the similarly-named male sexual organs of some Ascomycetes; among the Basidiomycetes they persist only in the Uredineae, and even in them are no longer functional and may be completely wanting. In nutrient solutions the spermatia may put out short germ-tubes, but are not capable of infecting the host plant.

The AECIDIA (Fig. 405) are cup-shaped fructifications, which when young are closed, but later open; from the ends of the hyphae numerous closely-associated chains of spores are abstricted. As a rule the enveloping layer or peridium of the aecidium is formed of thick-walled cells corresponding to the sterilised peripheral rows of spores. In *Phragmidium violaceum*, which occurs on the leaves of the Black-

berry, and has been fully investigated by BLACKMAN (78), the hyphae beneath the epidermis when about to give rise to an aecidium first cut off a sterile cell, which undergoes no further development, from their ends (Fig. 406 *A*). The cell below this increases in size ; it has at first only a single nucleus, but becomes binucleate

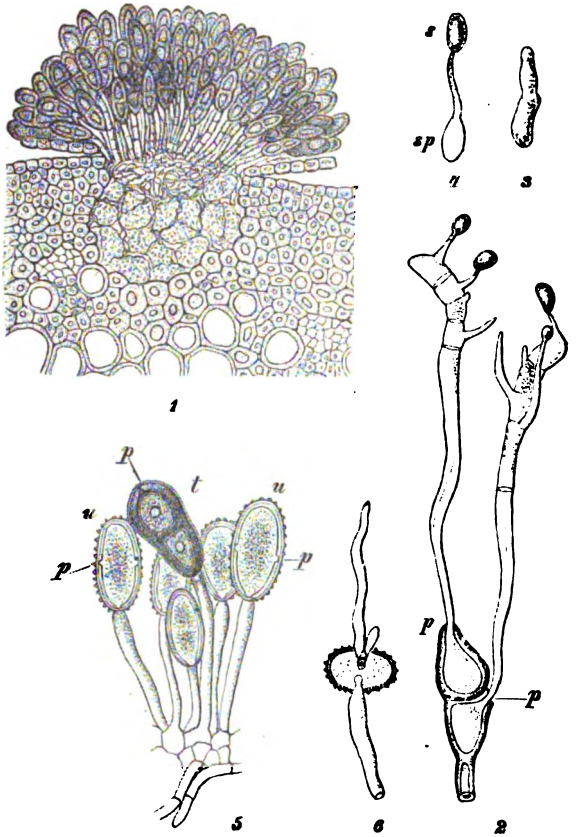


FIG. 403.—*Puccinia graminis*. *1*, Transverse section through a grass-haulm with group of teleutospores. *2*, Germinating teleutospore with two basidia. *3*, Vegetative, *4*, germinating basidiospore ; the latter has formed a secondary spore, not having been able to infect a host plant. *5*, A portion of a group of uredospores (*u*) and teleutospores (*t*) ; *p*, the germ-pores. *6*, Germinating uredospore. (*1*, *2*, *3*, *4* after TULASNE ; *5*, *6* after DE BARY. *1* × 150 ; *2* × circa 230 ; *3*, *4* × 370 ; *5* × 300 ; *6* × 390. From v. TAVEL, *Pilze*.)

by the passage of a nucleus into it from an adjoining mycelial cell. The two nuclei do not fuse. The binucleate cell undergoes successive divisions into a chain of spore-mother-cells, each of which has a pair of nuclei ; and from each spore-mother-cell an upper binucleate aecidiospore and a sterile intercalary cell, which is also binucleate but soon shrivels up, are derived by a transverse division (*B*, *C*).

According to CHRISTMAN (78) the development of the aecidiospores in *Phragmidium speciosum* (Fig. 407), which is parasitic on *Rosa*, proceeds somewhat

differently, and recent researches show that *Puccinia* and other genera agree. Here also the ends of the hyphae (*A*) divide into a terminal sterile cell and a lower fertile cell (*B*), but the fertile cells fuse in pairs with one another, the upper portions of the separating walls breaking down (*C*). The two nuclei lie side by side and divide simultaneously (conjugate division). Two of the daughter nuclei remain in the lower part and two pass to the upper portion of the dividing cell, and this upper portion is separated by a transverse wall as the first spore-mother-cell (*D*). In other respects the formation of the aecidiospores proceeds as described above. A peridium is not formed in *Phragmidium*, but in *Puccinia*, etc. it arises from the sterile peripheral chains of spores and from the sterile terminal cells of the central rows of spores.

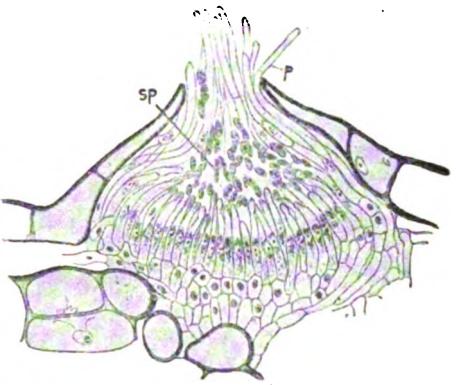


FIG. 404.—*Gymnosporangium clavariaeforme*. A spermogonium rupturing the epidermis of a leaf of *Crataegus*; *sp*, spermatia; *p*, sterile paraphyses. (After BLACKMAN.)

The ripe, binucleate aecidiospores (Fig. 406 *D*) are shed and infect a new host

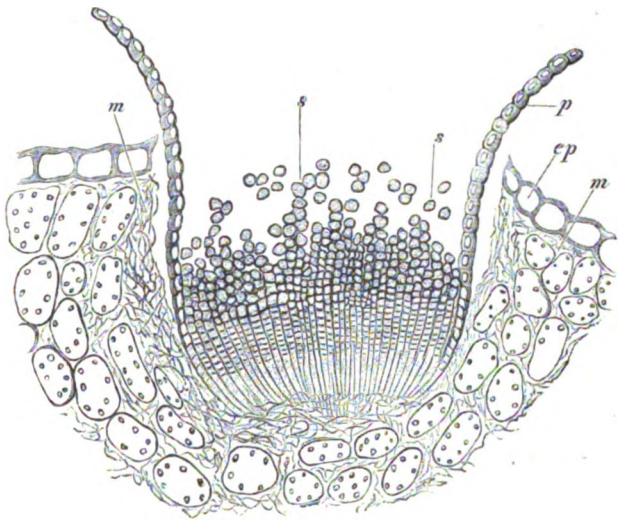


FIG. 405.—*Puccinia graminis*. Aecidium on *Berberis vulgaris*; *ep*. epidermis of lower surface of leaf; *m*, intercellular mycelium; *p*, peridium; *s*, chains of spores. (× 142.)

plant. Each spore gives rise to an intercellular mycelium which soon proceeds in the summer to bear UREDOSPORES or summer spores. These appear in small circular or linear groups and arise singly from the enlarging terminal cells of the hyphae

(Fig. 403, 5, 6). They have two nuclei like all the cells of the mycelium developed from the aecidiospore. They serve commonly to ensure the spread of the fungus in the summer. Later, either in the same or in distinct sori, the teleutospores are formed and in these the fusion of the two nuclei to a single one takes place; such a fusion as a rule is found to take place in the young basidium.

The two types of cell fusion in the formation of the aecidium are also known in other Uredineae, and must be regarded as replacing a formerly existing method of fertilisation. If we attempt to derive the Uredineae from the Ascomycetes the spermatia must be regarded as now functionless male cells, and the so-called fertile cells in the young aecidium as corresponding to carpogonia. Extending the comparison further the mycelium proceeding from the aecidiospore in the Uredineae and the uredospores and teleutospores borne on it, together with the basidia, formed by the latter, would together correspond to the diploid asexual generation (sporophyte) of the Ascomycetes. The basidiospores would thus correspond to the ascospores, while the mycelium proceeding from the basidiospores and ending in the production of aecidia would be equivalent to the haploid sexual generation (gametophyte). The agreement between Ascomycetes and Uredineae is also shown in the behaviour of the sexual nuclei which only become associated in pairs to fuse later in the young ascus or the young basidium.

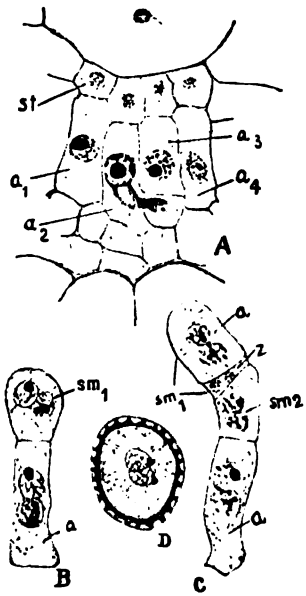


FIG. 406.—*Phragmidium violaceum*. *A*, Portion of a young aecidium; *st*, sterile cell; *a*, fertile cells; at a_2 the passage of a nucleus from the adjoining cell is seen. *B*, Formation of the first spore-mother-cell sm_1, from the basal cell *a* of one of the rows of spores. *C*, A further stage in which from sm_1 the first aecidiospore (*a*) and the intercalary cell (*z*) have arisen; sm_2, the second spore-mother-cell. *D*, Ripe aecidiospore. (After BLACKMAN.)

The three forms of spore borne by the sporophyte show, according to CHRISTMAN, a certain agreement in their development from the "basal cell" from which they arise; they may thus be regarded as morphologically equivalent.

The life-history of the Rust Fungi is thus a complicated one. The several forms of spore may appear in the course of the year on the one host, such Uredineae being termed autoecious. On the other hand, the spermogonia and aecidia may occur on one species of host plant, and the uredospores and teleutospores on another, often unrelated, plant. In these heteroecious species there is thus an alternation of host plants. There are also pleophagous heteroecious Uredineae in which the aecidia or the uredo- and teleuto-spores appear on a number of distinct host plants (79).

An example of an heteroecious Rust Fungus is afforded by *Puccinia graminis*, the Rust of Wheat. It develops its uredospores and teleutospores on all the green parts of Gramineae, especially of Rye, Wheat, Barley, and Oats. The aecidia and spermogonia of this species are found on the leaves of the Barberry (*Berberis vulgaris*). In the spring the hibernating double teleutospores give rise to transversely septate basidia, from which the four basidiospores are abstricted (Fig. 403, 2). These are scattered by the wind, and if they fall on the leaves of the

Barberry they germinate at once. The germ-tube penetrates the cuticle, and there forms a mycelium which gives rise to spermogonia on the upper side of the leaf and to aecidia on the under side (Fig. 405). On the rupture of the peridium the reddish-yellow aecidiospores are conveyed by the wind to the haulms and leaves of grasses, upon which alone they can germinate. The mycelium thus developed produces at first uredospores (Fig. 403, 5). They are unicellular, studded with warty protuberances, and provided with four equatorially-disposed germ-pores. Their protoplasm contains reddish-yellow fat globules. The uredospores are capable of germinating at once on the wheat, and thus the rust disease is quickly spread. Towards the end of the summer the same mycelium produces the dark brown, thick-walled teleutospores (Fig. 403, 1), which in this species are always double, being united in pairs. Each teleutospore is provided with one germ-pore, and on germination in the succeeding year the cycle is begun afresh. The mycelium of the uredo-form may hibernate in winter wheat, and

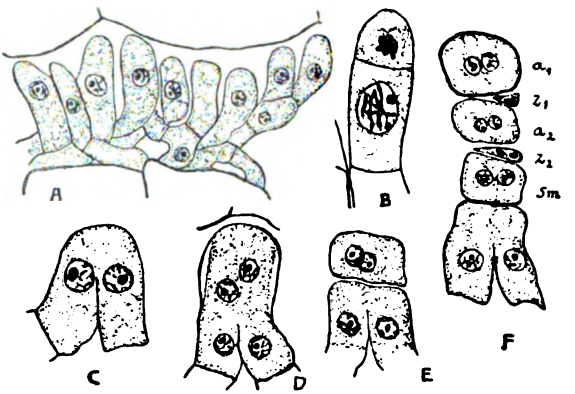


FIG. 407.—*Phragmidium speciosum*. *A*, The first rudiment of an aecidium beneath the epidermis of a leaf of *Rosa*. *B*, The division of the end-cell of a hypha into the upper, transitory, sterile cell and the lower fertile cell. *C*, Conjugation of two adjoining fertile cells. *D*, Later stage in which the first nuclear division is completed. *E*, Abstriction of the first aecidiospore mother-cell. *F*, Chain of aecidiospores (a_1, a_2) separated by intercalary cells (z_1, z_2); *sm*, the last-formed spore-mother-cell still undivided. (After CHRISTMAN.)

thus the rust may appear in the spring without the previous formation of basidiospores or of aecidia ([80]).

All Uredineae do not exhibit so complicated a course of development as *Puccinia graminis*. Rust fungi which produce all the forms of spore are termed eu-forms; those without uredospores, opsis-forms; those without aecidia, brachy-forms; those without aecidia and uredospores, micro-forms. In those Uredineae which no longer possess aecidia and spermogonia, the cells of the vegetative mycelium arising from the basidiospore are uninucleate, but subsequently, before the formation of the teleutospores, binucleate cells are found. The binucleate condition is attained, as has already been shown for several species, in the preparation for the development of the first uredospores or, when these are wanting, for the first teleutospores (*e.g.* in *Puccinia Malvacearum*). It results from the conjugation of two cells, as has already been described for the developing aecidium. This supports the homology of the three kinds of spore.

The genus *Endophyllum* ([81]), the species of which are parasitic on *Sempervivum*

and on *Euphorbia*, is simpler than the other Uredineae and forms neither uredospores nor teleutospores. The mycelium proceeding from the basidiospore consists of uninucleate cells and forms spermogonia and aecidia. The binucleate condition is attained as in *Phragmidium* by cell-fusions of the cells that will then give rise to the chains of aecidiospores. The mature aecidiospores behave like the teleutospores of the other Uredineae; their two nuclei fuse, and the spore germinates to form a basidium bearing four uninucleate basidiospores. This is preceded by a reduction division of the nucleus (Fig. 408). Possibly *Endophyllum* may be regarded as a primitive form. *Caeoma nitens* behaves in the same manner (81a).

Order 3. Auricularieae

The basidia, as in the case of the Uredineae, are transversely septate, with four spores. Only a few forms are included in this order. Among the most

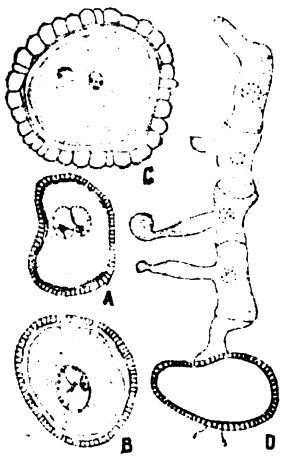


FIG. 408. — *Endophyllum Sempervivi.* *A*, Young aecidiospore, still bi-nucleate. *B*, Mature uninucleate spore. *C*, Germinating spore the nucleus of which has divided to form two. *D*, Aecidiospore which has germinated to form a young four-celled basidium. (After HOFFMANN.)

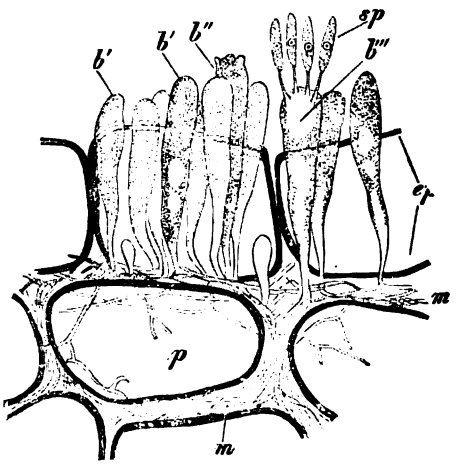


FIG. 409. — *Exobasidium Vaccinii.* Transverse section through the periphery of a stem of *Vaccinium*. *ep*, Epidermis; *p*, cortical parenchyma; *m*, mycelial hyphae; *b'*, protruding basidia without sterigmata; *b''*, with rudimentary sterigmata; *b'''*, with four spores. (× 620. After WORONIN.)

familiar is *Auricularia sambucina* (Judas's ear), found on old Elder stems. It has gelatinous, dark brown fructifications, which are shell-shaped and bear on their inner sides the basidial hymenium.

Order 4. Tremellineae

The basidia are longitudinally divided (Fig. 398). The hymenium is situated on the upper surface of the fructifications, which are generally gelatinous and irregularly lobed or folded. The few genera included in this order are saprophytic on decaying wood and tree-trunks, on the surface of which the fructifications are produced.

Order 5. Exobasidiineae

No distinctive fructifications are formed, and the basidia spring in irregular groups directly from the mycelium. They bear four spores on slender sterigmata. *Exobasidium Vaccinii* may be taken as a type of this form. The mycelium of this fungus, which is widely spread in Europe, is parasitic on the Ericaceae, especially on species of *Vaccinium*; it causes hypertrophy of the infected parts. The basidia are formed in groups under the epidermis, which they finally rupture (Fig. 409). In this genus, as in many others, accessory fructifications are developed, and spindle-shaped conidia are abstricted from the mycelium on the surface of the host plant, before the formation of the basidia.

Order 6. Hymenomycetes (70)

The basidia are undivided, and bear four spores at the apices of slender sterigmata (Fig. 410 *sp*). They are produced on fructifications, which bear definite hymenial layers, composed, in addition to the basidia, of paraphyses (Fig. 410 *p*), and also of sterile cystidia (*c*) or club-shaped tubes characterised by their larger diameter and more strongly thickened wall.

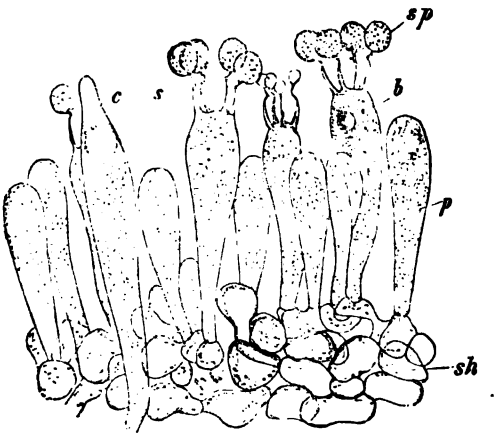


FIG. 410.—*Russula rubra*. Portion of the hymenium. *sh*, Sub-hymenial layer; *b*, basidia; *s*, sterigmata; *sp*, spores; *p*, paraphyses; *c*, a cystidium. (After STRASBURGER. × 540.)

The four spores are projected from the sterigmata by means of the osmotic pressure of the basidium to a distance of about $\frac{1}{10}$ mm.; they readily adhere to any surface. The paraphyses by separating the basidia facilitate the free shedding of the spores. The cystidia, according to KNOLL, are organs for secreting water and mucilage. They may have other functions in particular cases; thus in *Coprinus* they hold apart the gills and ensure the free fall of the spores (82).

In the Hymenomycetes, as in the most nearly related orders, special sexual organs are wanting and the basidia correspond to the asci of the Ascomycetes, and like these have, to begin with, two nuclei which then fuse. The question thus arises in what way the binucleate condition of the young basidium is brought about and what homologies exist with Ascomycetes in the course of development (83).

More recent investigations, especially those of KNIEP, have shown that in many Hymenomycetes a mycelium consisting of uninucleate cells is developed from the uni- or bi-nucleate basidiospores; that sooner or later before the formation of the fructification the binucleate condition is attained; that the pairs of nuclei show conjugate division; and that the binucleate condition is associated with the peculiar formation of clamp connections until the formation of the basidia. The clamp connections arise in the same way on the vegetative hyphae composed of elongated cells and on the shorter and stouter hyphae from which the hymenium is formed. In both cases a short protrusion forms about the middle of a terminal cell of a hypha (Fig. 411, 1). One of the two nuclei passes into the protrusion

and divides these (2, 3) simultaneously with the other nucleus of the pair. A transverse wall then forms just beneath the protrusion. The upper nucleus from the latter passes into the terminal cell of the filament, while the lower remains in the protrusion. This then becomes cut off from the terminal cell by a wall and fuses with the cell beneath into which the nucleus passes. By means of this clamp connection each of the two cells thus obtains a pair of nuclei derived from the original pair. It is possible that the significance of this round-about process lies in its ensuring the distribution of the sister nuclei to the two cells. The binucleate terminal cell gives rise to the basidium. The two nuclei fuse with one another and the resulting nucleus divides to give rise to the four nuclei for the spores (Fig. 411, 5, 6, 7).

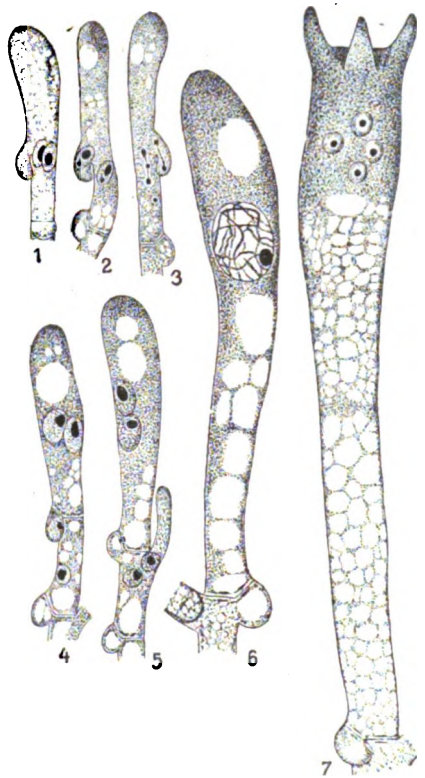


FIG. 411.—*Armillaria mucida*. Clamp formation and development of the basidium. *1*, Commencement of clamp formation in the binucleate terminal cell. *2*, One nucleus passing into the protrusion. *3*, Conjugate nuclear division. *4*, Clamp-cell and stalk-cell separated from the young basidium. *5*, Fusion of the two nuclei. *6*, Basidium with single nucleus resulting from fusion. *7*, Young basidium with the four basidiospore nuclei and the developing sterigmata. (After H. KNIEP.)

This clamp formation corresponds, according to KNIEP, to the hook-shape assumed in the developing ascus of many Ascomycetes; this is, however, limited to the ascogenous hyphae. Both groups contain forms without such arrangements, the development of the basidium or the ascus proceeding directly from the binucleate terminal cell of a hypha.

In the case of some Basidiomycetes the nucleus of the basidiospore divides into two and the mycelium with binucleate cells proceeds directly from this without any clamp formation. The genus *Hypochnus* behaves in this simpler fashion according to KNIEP.

The binucleate mycelium represents the diploid phase. The haploid stage commences in the basidium. Its end is indicated by the commencement of clamp connections, but in *Hypochnus* it is limited to the uninucleate stage of the basidiospore. As a result of the suppression of the sexual organs an alternation of generations is no longer present. It can at most be inferred from a phylogenetic point of view.

Most of the Hymenomycetes develop their profusely-branched mycelium in the humus soil of forests, in decaying wood, or on dying tree trunks, and produce fructifications, commonly known as toadstools, protruding from the

substratum. The mycelium of the forms vegetating in the soil spreads farther and farther, and dying in the centre as it exhausts the food material of the substratum, occupies continually-widening, concentric zones. In consequence of this mode of growth, where the development has been undisturbed, the fructifications, which appear in autumn, form the so-called fairy rings. A few Hymenomycetes are parasitic, and vegetate in the bark or wood of trees.

The Hymenomycetes are further classified according to the increasing complexity exhibited in the structure of their basidial fructifications.

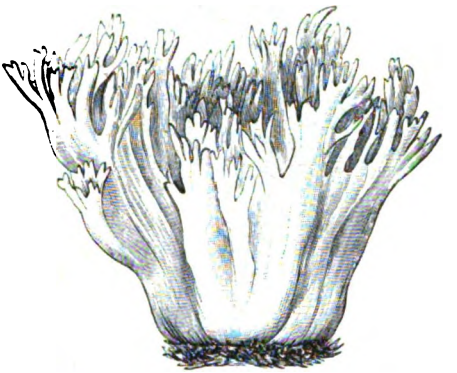


FIG. 412.—*Clavaria botrytis.* (Nat. size.)

1. In the group of the **Thelephoreae**, distinctive fructifications of a simple type are found. They form on the trunks of trees either flat, leathery incrustations bearing the hymenium on their smooth upper surfaces; or the flat fructifications become raised above the substratum and form bracket-like projections, which frequently show an imbricated arrangement, and bear the hymenium on the under side (*e.g. Stereum hirsutum*, common on the stems of deciduous trees). The edible *Craterellus cornucopioides* has peculiar black funnel-shaped fructifications.

2. The fructifications of the **Clavarieae** form erect whitish or yellow-coloured bodies, either fleshy and club-shaped or more or less branched, in a coral-like fashion. The larger, profusely-branched forms of this group are highly esteemed for their edible qualities; in particular, *Clavaria flava*, whose fleshy, yellow-coloured fructifications are often ten centimetres high, also *Clavaria botrytis* (Fig. 412), which has a pale red colour. *Sparassis crispa*, which grows in sandy soil in Pine woods, has fructifications half a metre in diameter, with compressed, leaf-like branches.

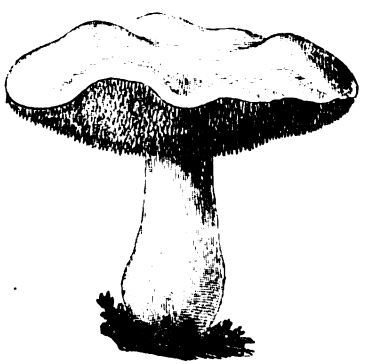


FIG. 413.—*Hydnum repandum.* (Reduced.)

3. The **Hydneae** have fructifications with spinous projections over which the hymenium extends. In the simpler forms the fructifications have the appearance of incrustations, with spinous outgrowths projecting from the upper surface; in other cases they have a stalk, bearing an umbrella-like expansion, from the under side of which the outgrowths depend. The latter form is exhibited by the edible fungi *Hydnum imbricatum*, which has a brown pileus 15 cm. wide, with dark scales on the upper surface, and *Hydnum repandum* (Fig. 413), with a yellowish pileus.

4. In the **Polyporeae**, a group containing numerous species, the stalked or sessile and bracket-shaped fructifications are indented on the under side with pit-

like depressions, or deep winding passages, or covered with a layer of tubes, closely fitted together and lined by the hymenium. To this family belongs the genus *Boletus*, occurring on the soil of woods, which has a large, thick-stalked pileus,

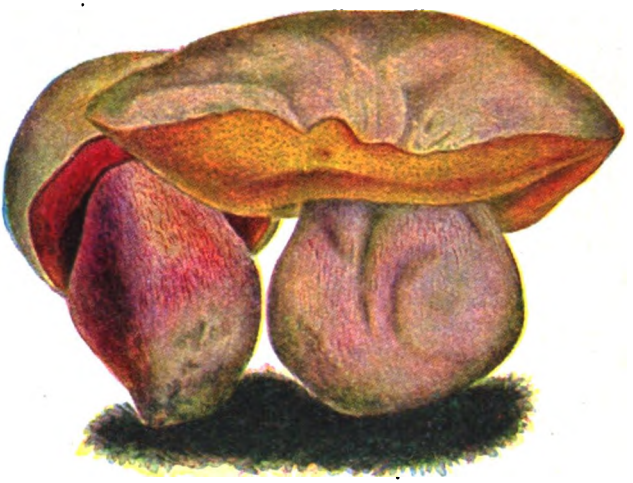


FIG. 414.—*Boletus Satanas*. (After KROMBHOLZ, ½ nat. size.) *Poisonous.*

covered on the under side with a layer of narrow dependent tubes. Although many species of this genus are edible (*e.g. B. edulis*, *B. badius*, *B. elegans*, and *B. luteus*), others are exceedingly poisonous, in particular *B. Satanas* (Fig. 414).

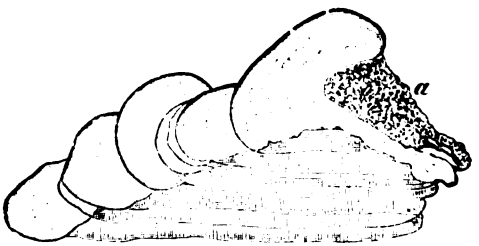


FIG. 415.—*Fomes igniarius*. Section through an old fructification, showing annual zones of growth. *a*, Point of attachment. (½ nat. size.)

FIG. 416.—*Psalliota campestris* (= *Agaricus campestris*). Mushroom. To the right a young fructification. (Reduced.)

The stalk of the latter fungus is yellow to reddish-purple, or has red reticulate markings, while the pileus, which may be 20 cm. wide, is yellowish-brown on its upper surface, but on the under side is at first blood-red, becoming later orange-red. *B. felleus* is unpleasant on account of its bitter taste; it differs from *B. edulis* in having bright rose-coloured tubes. Of the numerous species of the genus

Polyporus, Polyporus officinalis, with an irregularly tuberous white fructification, occurs on Larches in South Europe; it contains a bitter resinous substance and is also used in medicine. The mycelium of *Fomes fomentarius*, Touch-wood, is parasitic in deciduous trees, especially the Beech, and produces large, bracket or hoof-shaped, perennial fructifications, 30 cm. wide and 15 cm. thick. They have a hard, grey, external surface, but inside are composed of softer, more loosely-woven hyphae, and were formerly used for tinder. The narrow tubes of the hymenium are disposed on the under side of the fructifications in successive annual layers. *Fomes igniarius* (Fig. 415), which is often found on Oaks, and has a similar structure, has a rusty-brown colour, and furnishes, since it is much harder, a poorer quality of tinder.

Many parasitic Polyporeae are highly injurious to the trees attacked by them; thus *Fomes annosus* often causes the death of Pines and Spruce Firs. *Merulius lacrymans* (84), the Dry Rot fungus, is an exceedingly dangerous saprophytic species only rarely found wild in woods, but attacking and destroying the timber of damp houses, especially coniferous wood. The mycelium of this fungus forms large, white, felted masses with firmer branched strands which serve to conduct water and food substances. The hyphae have clamp connections. It gives rise to outspread, irregularly-shaped, pitted fructifications of an ochre or rusty-brown colour, and covered with a hymenial layer. Good ventilation of the infected space and dryness are the best remedial measures. *Merulius silvester* which occurs in woods is a related form.

FIG. 417.—*Amanita muscaria*. (½ nat. size.) POISONOUS.

5. The **Agaricineae**, which include the greatest number of species, have stalked fructifications, commonly known as Mushrooms and Toadstools. The under side of the pileus bears a number of radially-disposed lamellae or gills which are covered with the basidia-producing hymenium. In the early stages of their formation the fructifications consist of nearly spherical masses of interwoven hyphae, in which the stalk and pileus soon become differentiated. Many Agaricineae develop a so-called VELUM, consisting of a thin membrane of hyphal tissue which extends in young fructifications from the stalk to the margin of the pileus, but is afterwards ruptured, and remains as a ring of tissue encircling the stalk (Fig. 416). In *Amanita* (Figs. 417-419) the rudiments of the stalk and pileus are at first enclosed in a loosely-woven envelope, the VOLVA. In the course of the further development and elongation of the stalk the volva is ruptured, and its torn remnants form a ring or sheath at the base of the stalk, and in many cases are still traceable in the white scales conspicuous on the surface of the pileus.

Many of the Mushrooms found growing in the woods and fields are highly esteemed as articles of food. Of edible species the following may be named: the common Field-Mushroom, now extensively cultivated, *Psalliota campestris* (Fig. 416), with whitish pileus and lamellae at first white, then turning flesh-colour, and finally becoming chocolate-coloured; *Cantharellus cibarius*, having an orange-coloured pileus; *Lactaria deliciosa*, which has a reddish-yellow pileus and contains a similarly-coloured milky juice in special hyphal tubes; *Lactaria volema* has a brownish-red cap, a stout stalk, and white milky juice; *Tricholoma equestre* has the upper side of the pileus yellowish brown while elsewhere it is of a sulphur-yellow colour; *Lepiota procera*, whose white pileus is flecked with brown scales;

FIG. 418.—*Amanita phalloides*. (½ nat. size.)
VERY POISONOUS.

FIG. 419.—*Amanita mappa*. (½ nat. size.)
POISONOUS.

Amanita caesarea with an orange pileus bearing a few white scales and yellow lamellae. The brownish fructifications of *Armillaria mellea* are also edible. This species is a very injurious parasite, especially in Pine woods; its mycelium is characterised by the production of photogenic substances which cause the infected wood to appear phosphorescent in the dark (5). The mycelium forms, as a resting stage, blackish branched strands (rhizomorphs) beneath the bark or between the roots of the host plants.

Of the poisonous Agaricineae the following are best known: *Amanita muscaria* (Fig. 417), with white lamellae; *Amanita phalloides* (Fig. 418), often confounded with the Mushroom, with lighter or darker green pileus; *A. verna*, with white pileus, and *A. mappa* (Fig. 419), yellow or yellowish white. All three have white

gills and a swollen base to the stalk, which in the two first-named species bears a large lobed sheath. *Russula emetica*, with a red pileus and white lamellae; *Lactaria torminosa* having a shaggy, yellow or reddish-brown pileus and white milky juice.

Rozites gongylophora, found in South Brazil, is of special ecological interest. According to A. MÖLLER, this species is regularly cultivated in the nests of the leaf-cutting ants. Its mycelium produces spherical swellings at the ends of the hyphae, which become filled with protoplasm, the so-called Kohl-rabi heads, and serve the ants as food-material. The ants prevent the development of the accessory conidial fructifications peculiar to this fungus, and thus continually maintain the mycelium in their nests in its vegetative condition. The fructifications, which rarely occur in the nests, resemble those of *Amanita muscaria*, with which *Rozites* is nearly allied. According to HOLTERMAN, the mycelium of *Agaricus rajah* is cultivated in their nests by termites in tropical Asia ([85]).

ECONOMIC USES.—*Polyporus fomentarius* (FUNGUS CHIRURGORUM). *Polyporus officinalis* (=*Boletus laricis*) gives AGARICUS ALBUS, AGARICINUM, and ACIDUM AGARICINUM.

Order 7. Gasteromycetes ([70])

The Gasteromycetes are distinguished from the Hymenomycetes by their closed

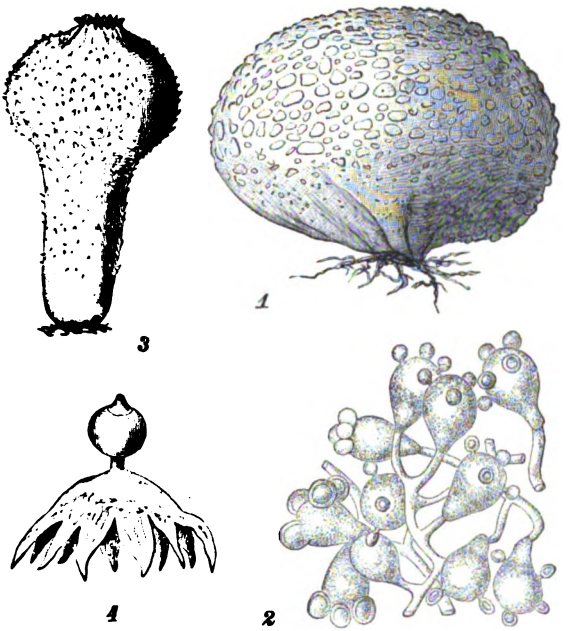


FIG. 420.—*1*, *Scleroderma vulgare*, fructification. *2*, Basidia of same. (After TULASNE.) *3*, *Lycoperdon gemmatum*. *4*, *Geaster granulosus*. (*1*, *3*, *4*, nat. size; *2*, enlarged.)

fructifications, which open only after the spores are ripe, by the rupture of the outer hyphal cortex or PERIDIUM. The spores are formed within the fructifications

in an inner mass of tissue termed the GLEBA; it contains numerous chambers, which are either filled with loosely-interwoven hyphae with lateral branches terminating in basidia, or their walls are lined with a basidial hymenium.

The Gasteromycetes are saprophytes, and develop their mycelium in the humus soil of woods and meadows. Their fructifications, like those of the Hymenomycetes, are raised above the surface of the substratum, except in the group of the Hymenogastreae, which possesses subterranean, tuberous fructifications resembling those of the Tuberaceae.

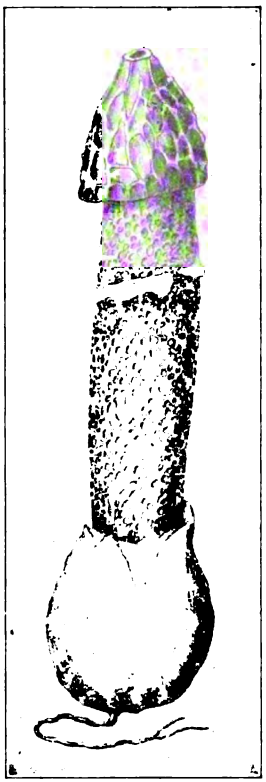


FIG. 421.—*Ithyphallus impudicus.* (½ nat. size.)

The fructifications of *Scleroderma vulgare* (Fig. 420, 1) have a comparatively simple structure. They are nearly spherical, usually about 5 cm. thick, and have a thick, light brown, leathery peridium which finally becomes cracked and ruptured at the apex. The gleba is black when ripe, and contains numerous chambers filled with interwoven hyphae which produce pear-shaped basidia with four sessile spores (Fig. 420, 2). This species, which is considered poisonous, is sometimes mistaken for one of the Truffle Fungi.

The genera *Bovista* and *Lycoperdon* (Fig. 420, 3) (Puffballs) have also spherical fructifications, which are at first white and later of a brown colour. In the last-named genus they are also stalked, and in the case of *Lycoperdon Bovista* may even become half a metre in diameter. The peridium is formed of two layers; the outer separates at maturity, while the inner dehisces at the summit. The hymenial layer of basidia, in the fungi of this group, lines the chambers of the gleba. The chambers are also provided with a fibrous capillitium consisting of brown, thick-walled, branched hyphae which spring from the walls, and aid in distributing the spores. The fructifications are edible while still young and white. When mature they contain urea.

In the related genus *Geaster* (Earth-star) (Fig. 420, 4) the peridia of the nearly spherical fructifications are also composed of two envelopes. When the dry fruit dehisces, the outer envelope splits into several stellate segments, and the inner layer of the peridium becomes perforated by an apical opening.

The highest development of the fructifications is exhibited by the **Phalloideae** (86), of which *Ithyphallus impudicus* (Stink-horn) is a well-known example.–This fungus is usually regarded as poisonous. It was formerly employed in a salve as a remedy for gout. Its fructification recalls that of the discomycetous *Morchella*, but it has quite a different manner of development. A fructification of this species of *Phallus* is about 15 cm. high. It has a thick, hollow stalk of a white colour and perforated with pores or chambers. Surmounting the stalk is a bell-shaped pileus covered with a brownish-green gleba which, when ripe, is converted into a slimy mass (Fig. 421). When young the fructification forms a white, egg-shaped body, and is wholly enveloped by a double-walled peridium with an inter-

mediate gelatinous layer. Within the PERIDIUM (also termed volva) the hyphal tissue becomes differentiated into the axial stalk and the bell-shaped pileus, carrying the gleba in the form of a mass of hyphal tissue, which contains the chambers and basidial hymenium. At maturity the stalk becomes enormously elongated, and pushing through the ruptured peridium raises the pileus with the adhering gleba high above it. The gleba then deliquesces into a dropping, slimy mass, which emits a carrion-like stench serving to attract carrion-flies, by whose agency the spores embedded in it are disseminated.

CLASS XV

Lichenes (Lichens) ([1, 51, 87-91])

The Lichens are symbiotic organisms; they consist of higher Fungi, chiefly the Ascomycetes, more rarely Basidiomycetes, and unicellular or filamentous Algae (Cyanophyceae or Chlorophyceae), living in intimate connection, and together forming a compound thallus or CONSORTIUM. Strictly speaking, both Fungi and Algae should be classified in their respective orders; but the Lichens exhibit among themselves such an agreement in their structure and mode of life, and have been so evolved as consortia, that it is more convenient to treat them as a separate class.

In the formation of the thallus the algal cells become enveloped by the mycelium of the fungus in a felted tissue of hyphae (Fig. 422). The fungus derives its nourishment saprophytically from the organic matter produced by the assimilating alga; it can also send haustoria into the algal cells, and so exhaust their contents. The alga, on the contrary, derives a definite advantage from its consortism with the fungus, receiving from it inorganic substances and water, and probably organic substances also.

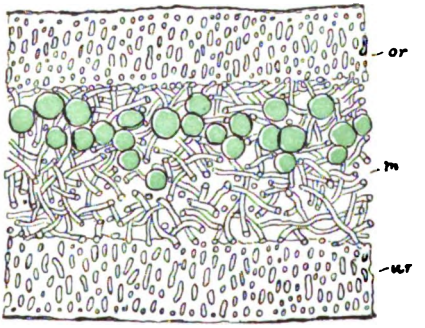


FIG. 422.—*Cetraria islandica.* Transverse section through the thallus; *or*, cortical layer of upper surface; *ur*, of the lower surface; *m*, medullary layer containing the green cells of the Alga, *Chlorococcum humicola.* (× 272.)

The main advantage in this mutualistic symbiosis is probably on the side of the fungus. This is especially the case in those Lichens which grow on bare rock, while in those growing on humus soil or on the bark of trees the fungus can, in part at least, derive its food saprophytically from the substratum. The Alga, however, exhibits active multiplication, and both it and the fungus can, as a result of the symbiosis, succeed in situations where neither could live alone.

The numerous Lichen acids, which are wanting only in the gelatinous Lichens, are products of metabolism peculiar to the group. Their production is due to the mutual chemical influence of the alga and fungus. They are deposited on the

surface of the hyphae in the form of crystals or granules. Their supposed use as a protection against snails appears, according to ZOPF, not to hold generally (86).

The Lichens are distributed in numerous species over the whole earth. They extend further than even the Mosses towards the poles and towards mountain summits. They attain their maximum development in moist Alpine regions where they sometimes cover the soil, rocks, and tree-trunks with a colonial vegetation or hang in beard-like masses from the branches of the trees. In the Arctic regions they may cover the soil and give rise to extensive tracts of Lichen tundra.

The simplest Lichens are the FILAMENTOUS, with a thallus consisting of algal filaments interwoven with fungal hyphae. An example of such a filamentous form is presented by *Ephebe pubescens*, which is found growing on damp rocks, forming a blackish layer.

Another group is formed by the GELATINOUS Lichens, whose thallus, usually foliaceous, is of a gelatinous nature. The algae inhabiting the thalli of the gelatinous Lichens belong to the families of the Chroococcaceae and Nostocaceae, whose cell walls are swollen, forming a gelatinous mass traversed by the hyphae of the fungus. The genus *Collema* is a European example of this group.

In both the filamentous and gelatinous Lichens the algae and the fungal hyphae are uniformly distributed through the thallus, which is then said to be unstratified or HOMOIOMEROUS.

The other Lichens have stratified or HETEROMEROUS thalli. The enclosed algae are usually termed GONIDIA. They are arranged in a definite GONIDIAL LAYER, covered, externally, by a CORTICAL LAYER, devoid of algal cells and consisting of a pseudo-parenchyma of closely-woven hyphae (Fig. 422). It is customary to distinguish the three following forms of heteromerous Lichens: CRUSTACEOUS LICHENS, in which the thallus has the form of an incrustation adhering closely to a substratum of rocks or to the soil, which the hyphae to a certain extent penetrate. FOLIACEOUS LICHENS (Fig. 426), whose flattened, leaf-like, lobed or deeply-cleft thallus is attached more loosely to the substratum by means of rhizoid-like hyphae (rhizines), springing either from the middle only or irregularly from the whole under surface. FRUTICOSE LICHENS (Fig. 424) have a filamentous or ribbon-like thallus branched in a shrub-like manner and attached at the base. They are either erect or pendulous, or may sometimes lie free on the surface of the substratum.

In nature the germinating spores of the Lichen Fungi appear to be capable of continuing their further development only when they are enabled to enter into symbiosis with the proper gonidia. For a few genera of Lichens, however, it has been determined that the fungi sometimes exist in nature without the presence of the algae; it has been shown that the tropical Lichen *Cora pavonia* (Fig. 431), whose fungus belongs to the order Hymenomycetes, may produce fructifications even when deprived of its alga; these have a form resembling those of the fungal genus *Thelephora*. Mycelia have

also been successfully grown from the spores of certain Lichen-forming Ascomycetes, cultivated without algae and supplied with a proper nutrient solution.

Many Lichens are able to multiply in a purely vegetative manner, by means of loosened pieces of the thallus, which continue their growth and attach themselves to the substratum with new rhizines. The majority of the heteromerous Lichens possess in the formation of SOREDIA another means of vegetative multiplication. In this process, small groups of dividing gonidia become closely entwined with mycelial hyphae and form small isolated bodies which, on the rupture of the thallus, are scattered in great numbers by the wind and give rise to new Lichens. Frequently the soredia arise in circumscribed receptacles (Fig. 423).

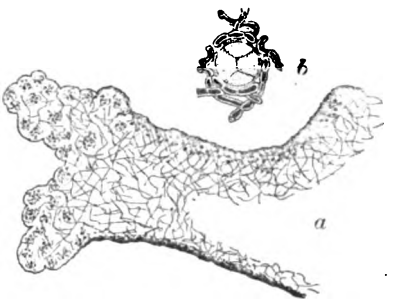


FIG. 423.—*Parmelia physodes.*
a, Formation of soredia; *b*, single soredium.

The fructifications of the Lichens are produced by the fungi, not by the algae, which are always purely vegetative.

1. Ascolichenes

Only a few genera of Lichens have flask-shaped perithecia, the fungus belonging to the Pyrenomycetes (*Endocarpon*, *Verrucaria*). Most genera produce, as the ascus-fruit of their fungus, cupular or discoid apothecia, sessile or somewhat sunk in the thallus. In structure they resemble those of the Discomycetes, and bear on their upper side an hymenium of asci and paraphyses. One of the commonest species of fruticose Lichens belonging to this group is *Usnea barbata*, the Beard Lichen, frequently occurring on trees and having large fringed apothecia (Fig. 424). *Ramalina fra.rinea*, which has a broad ribbon-shaped branched thallus and grows on trees, and the numerous species of *Roccella* found on the rocks of warmer coasts, have similar apothecia. *Cetraria islandica*, Iceland Moss (Fig. 425), occupies an intermediate position between the fruticose and foliaceous Lichens. It has a divided, foliaceous, but partially erect thallus, which is of a light bluish-green or brown colour, whitish on the under side, and bears the apothecia obliquely on its margin. This Lichen is found in mountainous regions and in the northern part of the Northern Hemisphere. The numerous species of *Parmelia* (Fig. 426) are foliaceous Lichens growing on trees and on rocks. *Graphis scripta* s a well-known example of the crustaceous Lichens; its greyish-white thallus occurs on the bark of trees, particularly of the Beech, on whose surface the apothecia are disposed as narrow, black furrows resembling writing.

A peculiar mode of development is exhibited by the genus *Cladonia*, whose primary thallus consists of small horizontal scales attached directly to the ground; from this thallus springs an erect portion, the PODETIUM, of varying form and

structure in the different species. In some cases the podetia are stalked and funnel-shaped, bearing on the margin or on outgrowths from it knob-like apothecia, which in *C. pyxidata* are brown, in *C. coccifera* (Fig. 427) bright red. In other

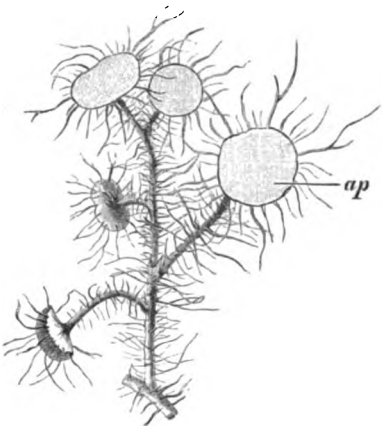


FIG. 424.—*Usnea barbata*. *ap*, Apothecium. (Nat. size.)

FIG. 425.—*Cetraria islandica*. *ap*, Apothecium. (Nat. size.) OFFICIAL.

species the erect podetia are slender and cylindrical, simple or forked; in *C. rangiferina*, Reindeer Moss, which has a world-wide distribution, particularly in the tundras of the North, the podetia are finely branched (Fig. 428), and bear the smal brown apothecia at the ends of the branches. The primary thallus of this species soon disappears.

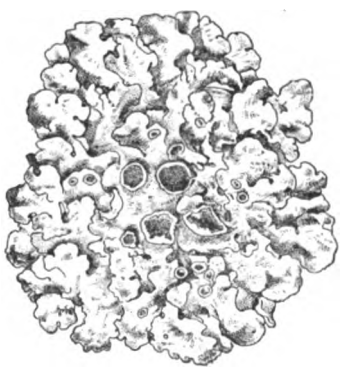


FIG. 426.—*Parmelia acetabulum*; grows on trees. (After REINKE.)

The ascus fructifications (apothecia or perithecia) of the Lichens originate, as STAHL and, more recently, BAUR (89) have shown, from carpogonia or female sexual organs which are frequently present in large numbers on young lobes of the thallus. The carpogonium (Fig. 429) is here a multicellular filament, the lower part of which is spirally coiled, while it continues above into a trichogyne composed of elongated cells and projecting from the surface of the thallus. All the cells are uninucleate and communicate with one another by means of pits. Those of the lower part of the filament contain abundant protoplasm. Apart from their multicellular nature these structures recall the carpogonia found in the Florideae. The spermatia which originate in spermogonia (Fig. 430) are presumably the male sexual cells. The spermatia develop in different ways (90). In some cases the inner wall of the spermogonium is lined with simple or branched hyphal branches from the ends of which the spermatia are abstricted (*Peltigera*, *Parmelia*). In other cases the spermogonium is at first filled with a hyphal tissue in which

cavities are formed later and the spermatia arise on very small and thin stalks from the cells lining the cavities (*Anaptychia*, *Physcia*, *Sticta*). The spermatia, embedded in a slimy mass, are shed from the spermogonium and conjugate with the adhesive tip of the trichogyne (Fig. 429 *B*). After conjugation the spermatia appear empty and their nucleus has disappeared. When this has taken place the cells

FIG. 427.—*Cladonia coccifera*. *t*, Scales of primary thallus. (Nat. size.)

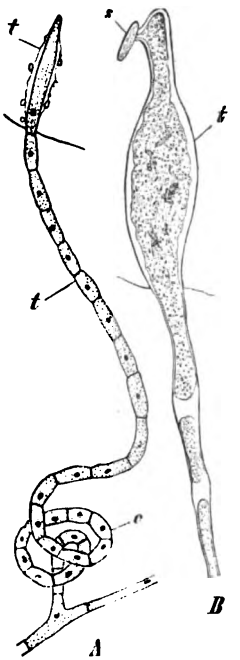


FIG. 429.—*Collema crispum*. *A*, carpogonium (*c*) with its trichogyne (*t*) (× 405). *B*, apex of the trichogyne with the spermatium (*s*) attached (× 1125). (After E. BAUR.)

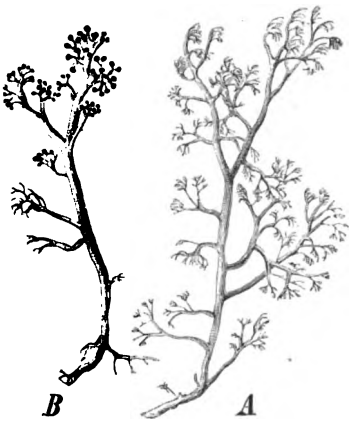


FIG. 428.—*Cladonia rangiferina*. *A*, sterile; *B*, with ascus-fruits at the ends of the branches. (Nat. size.)

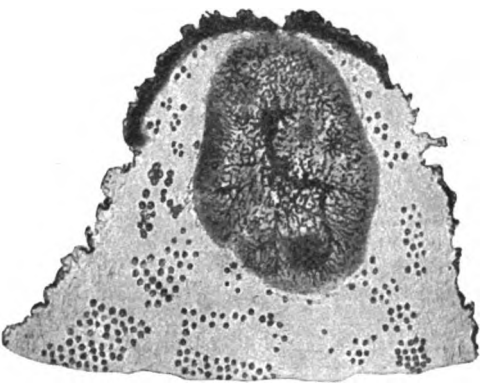


FIG. 430.—*Anaptychia ciliaris*. Ripe spermogonium. The dark round bodies within the thallus are the green algal cells. (× 192. After GLÜCK.)

of the trichogyne collapse, while the cells of the coiled carpogonium swell, undergo divisions, and form the ascogonium. From the latter the ascogenous hyphae which bear the asci are produced. The vegetative hyphae composing

the fructification and the paraphyses originate from hyphae which arise below the carpogonium. The fructification may arise from one or from several carpogonia. The behaviour of the sexual nuclei requires further investigation. Such carpogonia have been shown to give rise to the fructifications in a large number of genera. In other genera (*Peltigera*, *Solorina*) they are reduced, the trichogyne is wanting, and the reproduction is apogamous. Spermogonia are as a rule not found in these cases, or are, as in the case of *Nephromium*, clearly degenerating structures. It has been shown by A. MÖLLER that the spermatia of Lichens can germinate and produce a mycelium; but this is not inconsistent with their primitively sexual nature.

The behaviour of *Collema pulposum* is very remarkable. According to F. BACHMANN the spermatia arise in the interior of the thallus in small groups on the hyphae, and do not become detached. The elongated terminal cell of the trichogyne remains in the thallus but grows towards the spermatia and fuses with them [90a].

2. Basidiolichenes (Hymenolicehnes) [91]

The Hymenolichenes are represented by *Cora pavonia*, of which the genera *Dictyonema* and *Laudatea* are only special growth forms. This Lichen is widely spread in the tropics, growing on the soil or on trees. The fungus of this Lichen belongs to the family Thelephoreae (p. 463); its flat, lobed, and often imbricated fructifications are also found entirely devoid of Algae. In symbiosis with the unicellular Alga *Chroococcus* it forms the fructifications of *Cora pavonia* (Fig. 431), resembling those of the Thelephoras with a channelled, basidial hymenium on the under side. Associated symbiotically, on the other hand, with filaments of the blue-green Alga *Scytonema*, if the Fungus preponderates, it produces the bracket-like Lichens of the *Dictyonema* form, found projecting from the branches of trees with a semicircular or nearly circular thallus, having the hymenium on the under side. When the shape of the thallus is determined by the Alga, a Lichen of the *Laudatea* form occurs as felted patches of fine filaments on the bark of trees, with the hymenium on the parts of the thallus which are turned away from the light.

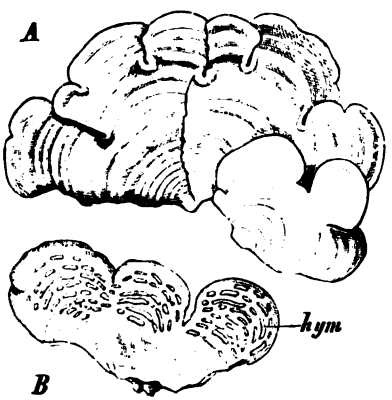


FIG. 431.—*Cora pavonia*. *A*, Viewed from above; *B*, from below; *hym*, hymenium. (Nat. size.)

OFFICIAL. — The only representative of the Lichens is *Cetraria islandica* (LICHEN ISLANDICUS). *Lobaria pulmonaria* is also used in domestic medicine.

The Manna Lichen (*Lecanora esculenta*) is a crustaceous Lichen that often covers the ground to a depth of 15 cm. in the Steppes and Deserts of Southern Russia, Asia Minor, and North Africa. The thallus falls into pieces the size of a pea, and is thus readily swept by the wind; it is used by the Tartars, who prepare earth-bread from it. *Cetraria islandica* also, when the bitter substances are removed by washing, may, owing to the abundant carbohydrate material (Lichen starch) it contains, be used to make bread as well as to prepare jelly. *Cladonia*

rangiferina is important as affording food for the Reindeer, and after the removal of bitter substances can be used as fodder for cattle. Alcohol is obtained from it in Norway.

Some species particularly rich in Lichen acids are used in the preparation of the pigments orseille and litmus; there are in the first place species of *Roccella* (especially *R. Montagnei*, *R. tinctoria*, *R. fuciformis*, and *R. phycopsis*) which are collected on the coasts of the warmer oceans, and the crustaceous lichen, *Ochrolechia tartarea*, in North Europe and America.

II. BRYOPHYTA (MOSSES AND LIVERWORTS) ([1, 92, 93-111])

The Bryophyta or Muscineae comprise two classes, the *Hepaticae* or Liverworts, and the *Musci* or Mosses. They are as regards their general segmentation Thallophyta, but are distinguished from them by the characteristic structure of their sexual organs, ANTHERIDIA and ARCHEGONIA, which are similar to those of the Pteridophyta. The Bryophyta and Pteridophyta are accordingly, in contrast to the Thallophyta, referred to collectively as *Archegoniatae*.

The Bryophytes as well as the Pteridophytes reproduce also asexually by means of SPORES provided with cell walls and adapted for dissemination through the air. These two modes of reproduction, sexual and asexual, occur in regular alternation, and are confined to sharply distinct generations: a sexual (gametophyte), provided with sexual organs, and an asexual (sporophyte), which produces spores. The sexual generation arises from the spore, the asexual from the fertilised egg. The number of chromosomes in the nuclei of the sporophyte is twice as great as in the nuclei of the gametophyte. The double number is acquired in the fusion of the sexual nuclei, while the reduction to one-half takes place in the division of the spore-mother-cells. This regular ALTERNATION OF GENERATIONS is characteristic of all Archegoniatae. In the Bryophyta the plant is the haploid generation, while the stalked capsule is the diploid sporophyte. In the Pteridophyta the gametophyte is a small thallus, while the sporophyte is a large cormophytic plant.

In the development of the SEXUAL GENERATION, the unicellular spore on germinating ruptures its outer coat or EXINE, and gives rise to a germ-tube. In the case of the Hepaticae the formation of the plant at once commences, but in most of the Musci a branched, filamentous PROTONEMA is first produced, composed of cells containing chlorophyll (Fig. 432). The green, filamentous protonema gives rise to branched, colourless rhizoids (*r*), which penetrate the substratum. The MOSS-PLANTS arise from buds developed on the protonema at the base of the branches. Protonema and moss-plant, in spite of the difference in appearance between them, together represent the sexual generation. Many Liverworts possess a thallus consisting of dichotomously-branching lobes (Figs. 446, 447), which

is attached to the substratum at its base or on the under side by means of rhizoids, thus repeating the vegetative structure of many Algae. In

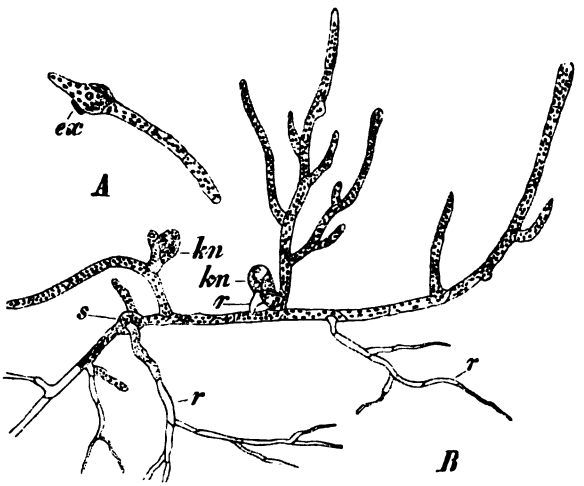


FIG. 432.—*Funaria hygrometrica*. *A*, Germinating spore; *ex*, exine. *B*, Protonema; *kn*, buds; *r*, rhizoids; *s*, spore. (Magnified. After MÜLLER-THURGAU.)

the higher Hepaticae, on the other hand, and in all the Musci, there exists a distinct differentiation into stem and leaves (Figs. 449, 456). Rhizoids spring from the lower part of the stem. True roots are wanting in the Bryophytes, which thus do not attain a higher grade of organisation than the differentiated thallus already met with among the Brown Algae, for example in *Sargassum*. The stems and leaves of Mosses are also anatomically of a simple structure; if conducting strands are present, they are composed merely of simple elongated cells. The sexual organs (antheridia and archegonia) are produced on the adult, sexual generation; in the thalloid forms on the dorsal side of the thallus; in the forms with stem and leaves at the apex of the stem or its branches.

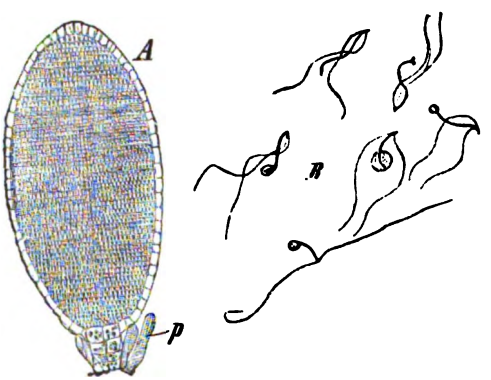


FIG. 433.—*Marchantia polymorpha*. *A*, Nearly ripe antheridium in optical section; *p*, paraphyses. *B*, Spermatozoids. (*A* × 90, B × 600. After STRASBURGER.)

The ANTHERIDIA (Fig. 433) or male sexual organs are stalked, ellipsoidal, spherical, or club-shaped, with thin walls formed of one layer of cells and enclosing numerous small, cubical cells, each of which becomes divided diagonally or transversely into two spermatozoid mother cells (94). At maturity the spermatozoid mother cells separate and are ejected from the antheridium, which ruptures at the apex. In the case of the Musci there is a terminal group of one or more cells with mucilaginous contents which on swelling burst the cuticle (Fig. 438 *A*); in the Liverworts the mucilaginous cells separate irregularly from one another and there is no defined cap of cells. By the dissolution of the enveloping walls of the mother cells the spermatozoids are set free as short, slightly-twisted filaments, bearing two long cilia close to the anterior end (Fig. 433).

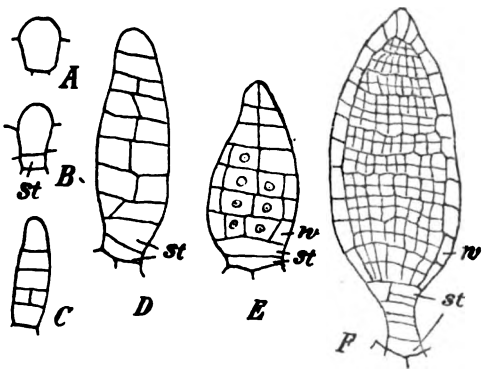


FIG. 434.—Development of the antheridium in *Fegatella conica*, one of the Marchantiaceae. *A*, Unicellular stage. *B*, The stalk-cell (*st*) cut off. *C*, *D*, Antheridium divided into a row of cells which in turn are divided by longitudinal walls. *E*, Cutting off of the layer of cells to form the wall (*w*). *F*, Advanced stage of development. (*A–E* × 400; *F* × 220. After BOLLETER.)

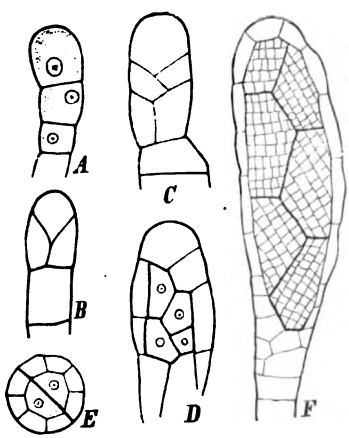


FIG. 435.—Development of the antheridium of a Moss. *Funaria hygrometrica*. *A*, Primordium of an antheridium divided into four cells. *B*, Formation of the apical cell from the uppermost cell. *C*, Division of the apical cell. *D*, The separation of the wall-layer and the cells that will give rise to the spermatogenous tissue. *E*, Same stage in transverse section. *F*, Older stage. (After D. CAMPBELL.)

The antheridium is developed from a single superficial cell; it is only in the case of *Anthoceros* (Fig. 443) that it is formed endogenously. In the lower Liverworts (Marchantiales) this cell becomes divided into transverse disc-shaped segments; each of these is divided by walls at right angles into four cells, and then tangential walls in these quadrants separate the peripheral cells of the antheridial wall from the internal cells, which give rise to the spermatogenous tissue (Fig. 434 *A-F*). In the higher Liverworts (Jungermanniales) the original cell is first divided into a row of three by transverse walls; the uppermost cell divides by a vertical wall, and in each of the two resulting cells two successively-formed walls separate

the wall and the cells which give rise to the spermatogenous tissue. In the Mosses (Musci), on the other hand, the antheridium develops by the segmentation of a two-sided apical cell, which is delimited by two oblique walls in the uppermost cell of a short row. Each of its segments is later divided into wall cells and an internal cell which contributes to the development of the spermatogenous cells (Fig. 435 *A-F*).

The archegonia (Fig. 436) are short-stalked, flask-shaped organs in which a venter and neck can be distinguished. The wall of the ventral portion encloses a large central cell, which divides shortly before maturity to give rise to the egg-cell and the ventral-canal-cell. The latter if situated at the base os the neck, just below a central row of neck-canal-cells, the number of which is lower in Liverworts (4-8) than in Mosses (10-30). The neck opens by the swelling of the mucilaginous contents of the uppermost cells which rupture the cuticle and often become rolled back as four lobes (Fig. 438 *B*) (95). The canal-cells become mucilaginous. Since water is essential for the process of fertilisation, this only takes place in land-forms after wetting by rain or dew. The movement of the spermatozoids towards the archegonia, and down the neck-canal to the egg-cell is directed by particular substances diffusing from the archegonium.

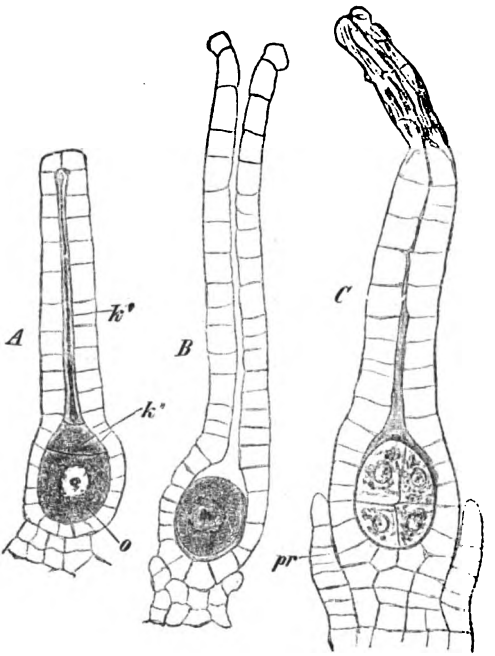


FIG. 436.—*Marchantia polymorpha*. *A*, Young, *B*, mature archegonium; *C*, fertilised archegonium, with dividing egg-cell. *k'*, Neck-canal-cell; *k''*, ventral-canal-cell; *o*, egg-cell; *pr*, pseudo-perianth. (× 540. After STRASBURGER.)

The spermatozoids of Mosses are attracted by cane-sugar solution, those of the Liverwort *Marchantia* also by proteid substances and by salts of potassium, rubidium, and caesium (96) (cf. p. 331).

The archegonium develops from a single superficial cell. In Liverworts this divides into a lower cell, which gives rise to the stalk, and an upper cell; the latter is divided by three longitudinal walls into three outer cells surrounding a central cell. The central cell is then divided by a transverse wall into a cap-cell and a completely enclosed internal cell. The outer cells give rise to the wall of

the venter and neck, while the inner cell divides to give rise to the egg-cell, ventral-canal-cell, and neck-canal-cells (Fig. 437). In Mosses, on the other hand, the original cell divides by inclined walls, and the segments of the resulting two-sided apical cell form the stalk. The terminal cell is then divided by three oblique walls and one transverse wall into a three-sided apical cell, truncated below; a central cell beneath this; and three peripheral wall-cells. The central cell gives rise to the egg-cell, ventral-canal-cell, and neck-canal-cells; the segments of the apical cell produce the wall of the neck and the uppermost neck-canal-cells. According to MELIN the Sphagnaceae occupy a middle position in that the stalk arises as in the Mosses, while the body of the archegonium is differentiated without a three-sided apical cell as in the Liverworts.

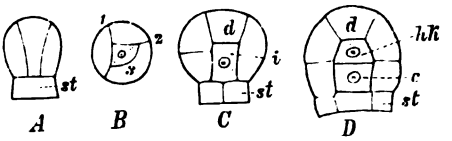


FIG. 437.—Development of the archegonium of a Liverwort. *A* (longitudinal section) and *B* (transverse section) showing the upper cell divided by three walls. *C*, The central cell divided into cap-cell (*d*) and internal cell (*i*). *D*, The internal cell divided into the cells which will give rise to the neck-canal-cells (*hk*), and the ovum and ventral-canal-cells (*c*) respectively; *st*, young stalk. (After GOEBEL.)

Antheridia and archegonia are homologous organs, as is shown by the occurrence of structures intermediate in nature; the ventral-canal-cell and neck-canal-cells are to be regarded as gametes which have become functionless. The ventral-canal-cell is as a rule smaller than the egg but may equal it in size. Occasionally several egg-cells may be developed in an archegonial venter, *e.g.* 4 or more in *Sphagnum* (93).

After fertilisation the zygote, without undergoing a period of rest, proceeds to divide and give rise to the embryo (Fig. 436 *C*). The embryo grows into the sporogonium which represents the asexual generation and remains throughout its life connected with the sexual generation; it obtains food-materials from the latter like a semi-parasitic plant. The sporogonium is a round or oval capsule, with a longer or shorter stalk, and containing numerous spores. These, as in Pteridophyta and Spermatophyta, arise in tetrads by the twice-repeated division of the spore-mother-cells, which have previously separated from one another and become rounded off.

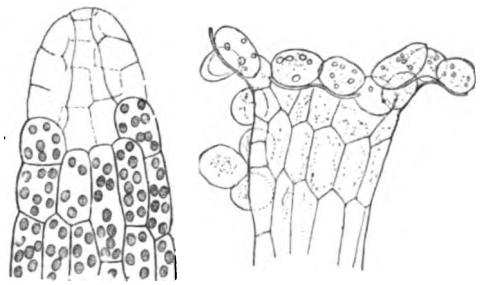


FIG. 438.—*A*, Summit of the empty antheridium of *Polytrichum* cut in half and showing the dehiscence cap. (After GOEBEL.) *B*, Opened neck of the archegonium of *Mnium undulatum*. (After ZIELINSKI.)

In the Mosses the lower part of the embryo penetrates into the, often much enlarged, tissue of the stalk of the archegonium and in some cases even into the

summit of the stem. This tissue along with the layer derived from the venter of the archegonium forms an investment that is later broken through by the growing embryo. The upper portion derived from the archegonial wall is carried up as the calyptra, while the lower portion forms a sheath round the base of the sporogonial stalk. The origin of the calyptra is similar in many Liverworts (*e.g.* in the Marchantiales); in others, however, the base of the embryo grows more or less deeply into the tissue of the thallus or stem below the archegonium. In special cases the tissue adjoining the archegonia forms a pouch-like structure (marsupium) enclosing the archegonium and embryo; this often grows down into the soil and represents a peculiar organ of protection and nutrition.

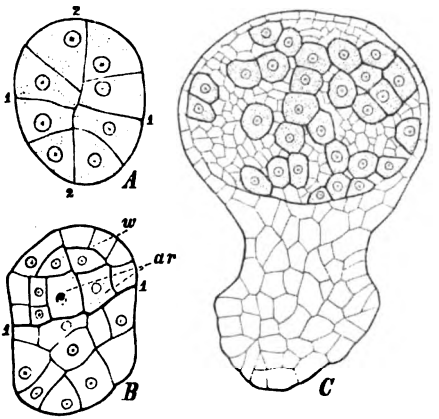


FIG. 439.—Development of the Sporogonium of *Corsinia marchantioides*, one of the Marchantiaceae. *A*, The zygote divided into 16 cells. *B*, The lower half of the embryo developing as foot, the upper as capsule; *w*, wall cells; *ar*, archesporium (× 170). *C*, Older sporogonium. The archesporium has given rise to spore-mother-cells and small sterile cells which in *Corsinia* do not develop further into elaters. (× 90.) (After K. MEYER.)

The development of the sporogonium exhibits a remarkable variety. In the lower Liverworts (Marchantiales) the zygote divides by transverse and longitudinal walls into 8, then by further radial walls into 16 cells, following on which comes division into external and internal cells by periclinal walls (Fig. 439). The foot and short stalk of the sporogonium come from the lower half of the embryo and the capsule from the upper half, the internal cells of which form the archesporium and give rise to the sporogenous tissue. The cells of this become in part spore-mother-cells, while others remain sterile and serve at first as nutritive cells to the developing spores (Fig. 439 *C*). Later these sterile cells usually grow into spindle-shaped structures with a spiral thickening of the wall (elaters); these on the opening of the capsule assist in the dispersion of the spores. Only in the Ricciaceae do all the internal cells become spore-mother-cells, the whole sporogonium being simplified to a spherical, unstalked capsule with a wall of one layer of cells.

In the higher Liverworts (Jungermanniales) the zygote first undergoes a number of transverse divisions; the lowest cell becomes sometimes after a few divisions an absorbent organ while the upper cells give rise to foot, stalk, and capsule. In addition to the spores, sterile cells, which usually develop into elaters, are formed from the sporogenous tissue.

The Anthocerotales are Liverworts which deviate considerably as regards the construction of the capsule from those described above and in some respects approach the Mosses (cf. p. 483).

In the Mosses the sporogonium has a columella which is an axile strand of sterile tissue serving for the conduction of materials; around this the archesporium is arranged as a, usually single, layer of cells. In the Sphagnales (Fig. 452 *C*) and the Andreaeales the archesporium extends as a dome over the summit of the

columella, while in the Bryales (Fig. 458) it constitutes an open cylinder around the columella. The elongated embryo is composed of segments which in the Sphagnales arise by transverse division of the zygote and in other Mosses are cut

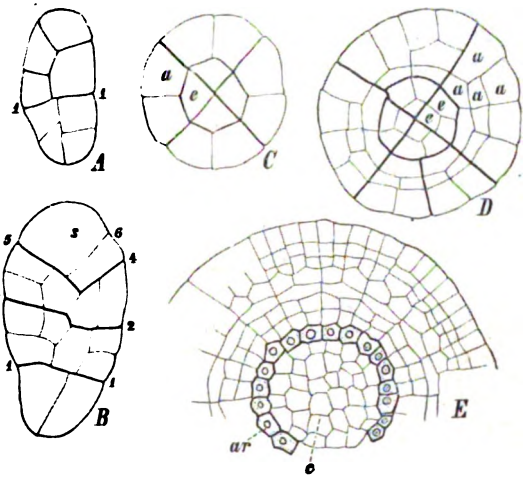


FIG. 440.—Development of the sporogonium of the Moss, *Funaria hygrometrica*. *A*, *B*, Longitudinal sections showing first stages in the development from the zygote *s*, apical cell. *C-E*, Transverse sections: *C*, division into endothecium (*e*) and amphithecium (*a*); *D*, further divided stage; *E*, older sporogonium, in the endothecium of which the outermost layer is distinct as the archesporium (*ar*) from the columella (*c*). (After CAMPBELL.)

off from a two-sided apical cell. In each transverse segment a longitudinal division follows, and in the resulting quadrants there is a separation of outer cells (amphithecium) from internal cells (endothecium) (Fig. 440). In the Sphagnales only, the archesporium arises as the innermost layer of the amphithecium; in all other Mosses it is the outermost layer of the endothecium. It gives rise exclusively to spores, no sterile cells being formed (Fig. 441).

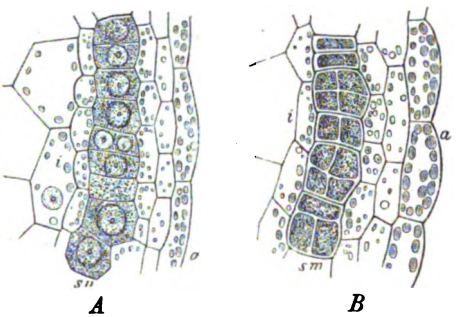


FIG. 441. — *Funaria hygrometrica*. Transverse section through the archesporium (*A*, *su*), and the groups of still connected spore-mother-cells derived from it (*B*, *sm*). (After GOEBEL.)

The Bryophyta are characterised by a great power of regeneration from cut portions of all the organs. Vegetative reproduction by means of gemmae, etc., is widespread; they arise on the thallus, on stems, on leaves, and on the protonema in a great variety of ways, becoming separated later (97).

There are difficulties in the way of the phylogenetic derivation of the Bryophyta from any definite group of Algae. Between the Bryophytes on the one hand, and

the higher Green Algae and Characeae on the other, no transitional forms are known. Morphological comparison points rather to a connection between the Bryophyta and the Brown Algae, the multilocular gametangia of which (in some genera already differentiated into oogonia and antheridia) may be regarded as homologous structures leading to the archegonia and antheridia of the Archegoniatae. Thus the antheridium of the lower Liverworts shows a cellular construction in agreement with that of the gametangia of Brown Algae (cf. Figs. 434, 354, 356); it is distinguished by the possession of a sterile, protective layer of cells forming the wall, and the differentiation of this can be regarded as an adaptation to a terrestrial mode of existence. Further, among the Brown Algae, in *Dictyota*, there is an alternation of generations agreeing with that of Bryophyta, although the gametophyte and sporophyte are similar in their vegetative structure. The tetrasporangia of the sporophyte of *Dictyota* correspond to the spore-mother-cells of the sporophyte of the Bryophyta; their endogenous position in the latter may be related to the influence of a terrestrial mode of life. While the form of the gametophyte in the thalloid Liverworts shows many points in common with the thallus of certain Brown Algae, the sporophyte of the Bryophyta proceeds early to the development of its spores, and ceases growth without a segmentation into vegetative organs. It thus becomes essentially different from the gametophyte (98).

With the exception of a few forms which have secondarily assumed an aquatic life, the Bryophyta in contrast to the Algae are land-plants and exhibit corresponding adaptations in their structure. Thus all the above-ground parts are covered with a cuticle. The small size of the Bryophyta as compared with Pteridophyta stands in connection with their simple cellular construction from which true vessels are absent. True roots are also wanting. Some are minute plants, while the largest Mosses, represented by the Dawsonieae of New Zealand, have leafy stems attaining a height of 50 cm.

The two very distinct classes of Bryophytes may be briefly characterised as follows:

1. *Hepaticae* (Liverworts).—The sexual generation, with poorly developed and generally not distinctly differentiated protonema, is either a dichotomously-divided thallus or is developed as a leafy and, with few exceptions, dorsiventral shoot. In the majority of Hepaticae, in addition to spores, the capsule produces also elaters; only in one order, Anthoceroteae, does the capsule have a columella.

2. *Musci* (Mosses).—The protonema of the sexual generation is usually well developed and distinctly defined, and the moss plant is always segmented into stem and leaves. The leaves are arranged spirally in polysymmetrical, less frequently in bisymmetrical, rows. The capsule is always without elaters, but with a columella.

Fossil Bryophyta.—The Liverworts are more primitive in their organisation than the Mosses and appear to be more ancient, since their fossil remains are occasionally met with back to the Carboniferous period, while the earliest known Mosses are from the Upper Cretaceous. Most fossil Bryophytes are from the Tertiary rocks and closely resemble existing forms.

CLASS I

Hepaticae (Liverworts) ([1, 92, 93, 99-104])

Most Liverworts inhabit moist situations and have a corresponding hygrophilous structure. True aquatic forms are, however, only sparingly represented. Some delicate Jungermanniaceae grow among Mosses. Other less numerous forms live in extremely dry habitats on the bark of trees, on rocks or on the ground; these have xerophilous structure and arrangements for the storage of water. Among the epiphytes those that grow on leaves in tropical forests (epiphyllous liverworts) are noteworthy. As a rule the Liverworts play an inconsiderable part in the composition of cryptogamic plant-formations.

The rhizoids of many Liverworts, especially of the Jungermanniaceae, and the non-chlorophyllous tissue of the thallus of some Marchantiaceae are frequently inhabited by endophytic fungi (*e.g.* by hyphae of *Mucor rhizophilus*); these do no serious injury but appear to be of no special benefit ([100]).

The Hepaticae are divided, according to the structure of the sporogonium and the segmentation exhibited by the sexual plant, into three orders, the Anthocerotales and Marchantiales being exclusively thalloid, while the Jungermanniales include both thalloid and dorsiventral foliose forms and, in the group of the Haplomitrieae, radially-constructed foliose forms.

Order 1. Anthocerotales ([101])

This isolated group, including only a few forms, may be regarded as a primitive order of Bryophyta. The sporogonium is characterised by a more complicated internal construction than in the other Liverworts, in which it has undergone progressive simplification.

The gametophyte has the form of an irregular, disc-shaped thallus, which is firmly anchored to the soil by means of rhizoids. The cells of the thallus contain, in contrast to those of other Bryophyta, a single large chloroplast with a pyrenoid. On the lower surface, and less commonly on the upper, stomata occur. The antheridia arise singly or in groups of two to four, by the division of a cell lying below the epidermis (Fig. 443); they remain enclosed in cavities beneath the upper surface of the thallus until maturity. The origin of the antheridia thus differs from what is the case in all other Archegoniatae in being endogenous; a superficial cell divides into an outer segment, forming the roof of the cavity, and an inner one, which becomes the mother-cell of the antheridia. The cavity opens at maturity by mucilage formation in the cells of the outer wall. The archegonia are sunk in the upper surface of the thallus; after fertilisation they become covered over by a many-layered wall (marsupium) formed by the growth of the adjoining tissue. This enveloping wall is afterwards ruptured by the elongating capsule, and forms a sheath at its base. The sporogonium consists of a swollen foot and a long, pod-shaped capsule; it has no stalk. The superficial cells of the foot grow out into rhizoid-like papillae. The capsule splits longitudinally into two valves, and has a central hair-like columella formed of a few rows of sterile cells (Fig. 442). The columella does not extend to the apex of the capsule, but is surmounted by a narrow layer of sporogenous cells. Elaters also occur; they are multicellular, variously shaped, and often forked. The

sporogonia, unlike those of all other Hepaticae, do not ripen simultaneously throughout their whole length, but from the tips downwards, and continue to elongate by basal growth after emerging from the archegonia. The wall of the

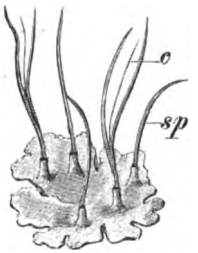


FIG. 442. — *Anthoceros laevis.* *sp*, Sporogonium; *c*, columella. (Nat. size.)

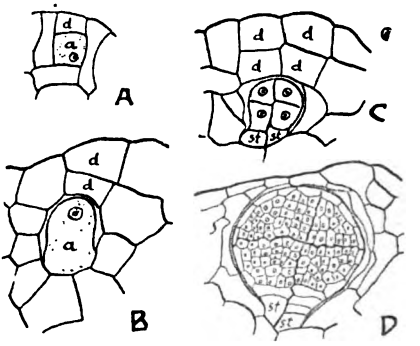


FIG. 443.—*Anthoceros Pearsoni.* Development of the endogenous antheridium. *d*, Covering cells; *st*, stalk-cells; *a*, young antheridium. (After D. CAMPBELL.)

sporogonium possesses stomata, which do not occur in other Liverworts; chlorophyll is present in its cells.

On the under side of the thallus, slit-like openings, formed by the separation of the cells, lead into cavities filled with mucilage. *Nostoc* filaments penetrate into these cavities, and develop into endophytic colonies ([101a]).

Order 2. Marchantiales ([102])

The Liverworts included in this order in many genera have a decidedly complicated structure. *Marchantia polymorpha*, found growing on damp soil, may serve as an example. It forms a flat, deeply-lobed, dichotomously-branched thallus, about two centimetres wide, and having an inconspicuous midrib (Fig. 445 *A*, Fig. 446 *A*). From the under side of the thallus spring unicellular rhizoids, some of which have smooth walls and serve mainly to attach the thallus, while others have conical thickenings projecting into the cell-cavity (Fig. 31); these peg-rhizoids are collected to form a wick-like strand below the midrib. The thallus is provided also with ventral scales, consisting of a single layer of cells. The dorsiventrality of the thallus is further shown by its complicated anatomical structure. With the naked eye it may be seen that the upper surface of the thallus is divided into small rhombic areas. Each area is perforated by a central air-pore leading into a corresponding air-chamber immediately below (Fig. 95 *A*, *B*). The lateral walls of the air-chambers determine the configuration of the rhombic areas. The air-pore in the roofing wall of each chamber is in the form of a short canal, bounded by a wall formed of several tiers of cells, each tier comprising four cells. Numerous short filaments, consisting of rows of nearly spherical cells containing chlorophyll grains, project from the floor of the air-chambers and perform the functions of assimilating tissue. Chlorophyll grains are found also in the walls and roof of the chambers, but only in small numbers. The intensity of the illumination exercises a great influence on the formation of air-chambers; when the illumination is very weak they may not

occur at all. The epidermis on the under side of the thallus is formed of one layer of cells. The tissue below the air-chamber layer is devoid of chlorophyll, and consists of large parenchymatous cells, which serve as storage cells.

Small cup-shaped outgrowths, with toothed margins, the gemmiferous receptacles or gemma-cups, are generally found situated on the upper surface of the thallus over the midribs (Fig. 445 *b*). These contain a number of stalked gemmae, flat, biscuit-shaped bodies of a green colour. The gemmae arise by the protrusion and repeated division of a single epidermal cell (Fig. 444); at maturity they become detached from the stalk (at *x*, Fig. 444 *D*). They are provided with two growing points, one at each of the marginal constrictions, from which their further development into new plants proceeds. On cross-section (*E*) they are seen to be composed of several layers of cells; some of the cells are filled with oil globules (*D*, *o*), while from other colourless cells rhizoids develop. Cells containing oil are also present in the mature thallus, and are of frequent occurrence in all the Hepaticae. By means of the abundantly-developed gemmae *Marchantia* is enabled to multiply vegetatively to an enormous extent. The dorsiventrality of the plants developed from the gemmae is determined by the influence of light.

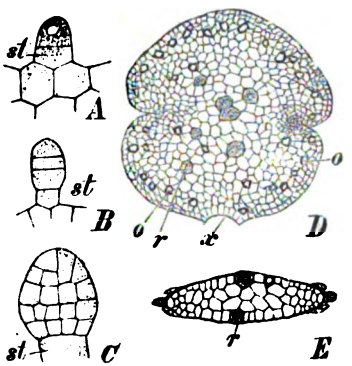


FIG. 444. — *Marchantia polymorpha*. *A*-*C*, Successive stages in the formation of a gemma; *st*, stalk-cell; *D*, surface view; *E*, transverse section of a gemma; *x*, point of attachment to stalk; *o*, oil cells; *r*, colourless cells with granular contents, from which the rhizoids will develop. (*A*-*C* × 275; *D*-*E* × 65. After KNY.)

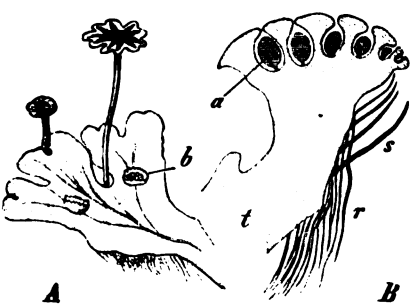


FIG. 445. — *Marchantia polymorpha*. *A*, A male plant, with antheridiophores and gemma-cups *b* (nat. size). *B*, Section of young antheridiophore; *a*, antheridia; *t*, thallus; *s*, ventral scales; *r*, rhizoids. (Somewhat magnified.)

The sexual organs, antheridia and archegonia, are borne on special erect branches of the thallus. The reproductive branches, which are contracted below into a stalk, expand above into a profusely-branched upper portion. In this species, which is dioecious, the antheridia and archegonia develop on different plants. The branches producing the male organs terminate in lobed discs, which bear the antheridia on their upper sides in flask-shaped depressions, each containing an antheridium (Fig. 445 *B*). The depressions, into each of which a narrow canal leads, are separated from each other by tissue provided with air-chambers. (The structure of the antheridia and spermatozoids is illustrated by Figs. 433, 434, and the accompanying description.) The spermatozoids collect in a drop of water on the disc, the margin of which serves to retain the water.

The female branches terminate each in a nine-rayed disc (Fig. 446 *A*). The upper surface of the disc, between the rays, becomes displaced downwards in the process of

growth, and, as the archegonia are borne on these portions, they seem to arise from the under side of the disc. The archegonia are disposed in radial rows between the

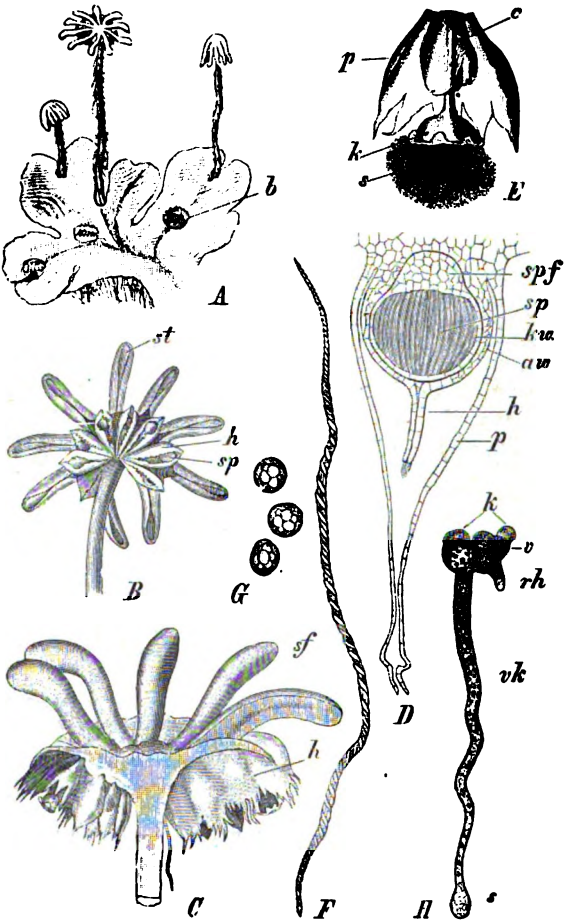


FIG. 446.—*Marchantia polymorpha*. *A*, A female plant, with four archegoniophores of different ages; *b*, gemma-cups (nat. size). *B*, Under side of receptacle; *st*, rays; *h*, sheath; *sp*, sporogonium (×8). *C*, Half of a receptacle, divided longitudinally (×5). *D*, Longitudinal section of a young sporogonium; *spf*, the foot; *sp*, sporogenous tissue; *kw*, wall of capsule; *aw*, wall, and *h*, neck, of archegonium; *p*, pseudo-perianth (×70). *E*, Ruptured sporogonium; *k*, capsule; *s*, spores and elaters; *p*, pseudo-perianth; *c*, archegonial wall (×10). *F*, An elater. *G*, Ripe spores (×315). *H*, Germinating spore (*s*); *vk*, germ tube; *k*, germ-disc, with the apical cell *v* and rhizoid *rh* (×100). (*C*, *E* after BISCHOFF; *B*, *D*, *F-H* after KNY.)

rays, each row being surrounded by a toothed lamella or sheath (perichaetium) (*B*, *C*, *h*). For structure of the archegonia see Fig. 436 and description.

Fertilisation takes place during rain, the raindrops splashing the liquid on the male discs which contains the spermatozoids, on to the female receptacles.

The epidermal cells of the latter project as papillae and constitute a superficial capillary system in which the spermatozoids are conducted to the archegonia.

The fertilised egg-cell gives rise to a multicellular embryo (Fig. 436 *C*), and this, by further division and progressive differentiation, develops into a stalked oval SPOROGONIUM. The capsule of the sporogonium is provided with a wall consisting of one layer of cells except at the apex, where it is two-layered ; the cell-walls have thickened bands. The capsule ruptures at the apex, the lid falling off and the wall splitting into a number of recurved teeth. The ripe capsule, before the elongation of the stalk, remains enclosed in the archegonium wall (Fig. 446 *D*, *aw*), which, for a time, keeps pace in its growth with that of the capsule. As the stalk elongates, the archegonial wall or calyptra is broken through and remains behind, as a sheath, at the base of the sporogonium (*E*, *c*). The capsule is surrounded also by the pseudo-perianth, an open sac-like envelope which grows, before fertilisation, out of the short stalk of the archegonium (Fig. 436

A *B* *C*

FIG. 447. — *A*, *Riccia fluitans*; submerged floating form. *B*, *Riccia natans*; land form. *C*, *Riccia natans*; floating form with long ventral scales. (Nat. size. *B* after GOEBEL. *C* after BISCHOFF.)

C, *pr* ; Fig. 446 *D*, *E*, *p*). The capsule contains spores and elaters (Fig. 446 *F*, *G*).

Marchantia was formerly used in the treatment of diseases of the liver ; this fact explains the origin of the name Liverwort.

The **Ricciaceae** (103) exhibit an extensive simplification of the sporogonium and connect on as reduced forms to the more simply constructed Marchantiaceae. The dichotomously-lobed or cleft thallus forms small rosettes, and grows on damp or marshy soil. *Riccia natans* (Fig. 447 *C*) is found floating, like Duckweed, on the surface of stagnant water. *Riccia fluitans*, on the other hand, lives wholly submerged, and has narrow, more profusely-branching, thalloid segments (Fig. 447 *A*). These two aquatic species can, however, grow on marshy soil, and then form flat rosettes (Fig. 447 *B*). The Riccias are provided with fine rhizoids springing from the under side of the thallus, and possess, in addition, a row of transversely disposed ventral scales, consisting of a single layer of cells, which also assist in the absorption of nourishment. Both organs are wanting in the submerged form of *Riccia fluitans*.

The antheridia and archegonia are sunk in the surface of the upper side of the thallus. From the fertilised egg-cell is developed a spherical sporogonium which has no stalk. The wall of the sporogonium consists of a single layer of cells ; it becomes disorganised during the ripening of the spores, which are eventually set free by the rupture and disintegration of the venter and the surrounding cells of the thallus. There are no elaters.

Order 8. Jungermanniales

These are usually small forms which grow on the ground or on tree-trunks, and in the tropics on the surface of living leaves. In the simplest forms of this order the thallus is broadly lobed, similar to that of *Marchantia* (*e.g. Pellia epiphylla*, frequently found on damp ground); or, like that of *Riccia fluitans*, it is narrow and ribbon-shaped, and at the same time profusely branched (*e.g. Metzgeria furcata*, Fig. 94). In other forms, again, the broad, deeply-lobed thallus has an evident midrib, and its margins, as in the case of *Blasia pusilla* (Fig. 448), exhibit an incipient segmentation into leaf-like members. The majority of Jungermanniaceae, however, show a distinct segmentation into a prostrate or ascending, dorsiventral stem and leaves (Fig. 449). The latter consist of one layer of cells without a midrib, and are inserted with obliquely directed laminae in two rows on the flanks of the stem. Many

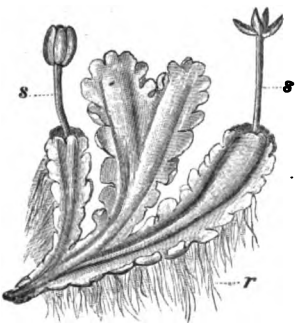


FIG. 448.—*Blasia pusilla*. *s*, Sporogonium; *r*, rhizoids. (× 2.)

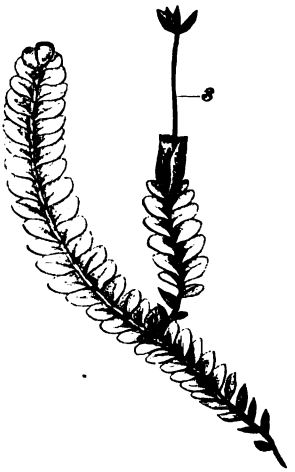


FIG. 449.—*Plagiochila asplenioides*. *s*, Sporogonium. (Nat. size.)

genera (*e.g. Frullania Tamarisci*, a delicately-branched Liverwort of a brownish colour occurring on rocks and tree-trunks) have also a ventral row of small scale-like leaves or amphigastria (Fig. 450). The dorsal leaves are frequently divided into an upper and lower lobe. In species growing in dry places, like *Frullania Tamarisci*, the lower lobe may be modified into a sac, and serves as a capillary water-reservoir. The leaves regularly overlap each other; they are then said to be overshot, when the posterior edges of the leaves are overlapped by the anterior edges of those next below (*Frullania*, Fig. 450), or undershot, if the posterior edges of the leaves overlap the anterior edges of the leaves next below (*Plagiochila*, Fig. 449).

The long-stalked sporogonium is also characteristic of this order; it is already fully developed before it is pushed through the apex of the archegonial wall by the elongating delicate stalk. It has a spherical capsule which on rupturing splits into four valves (Figs. 448, 449). No columella is formed in the capsule; but in addition to spores it always produces elaters. In some genera (*Pellia Aneura*) there are special elaterophores which consist of groups of sterile cells resembling the elaters. The wall of the capsule (usually two or several cells thick) consists of cells with annular or band-like thickenings, or the walls are uniformly

thickened with the exception of the outermost walls. Dehiscence is dependent on the cohesive power of the water in these cells pulling the outer walls into the cavity.

According to the position of the sexual organs and sporogonium the Jungermanniales are divided into groups. 1. In the **Anakrogynae** the apex is not used up in the formation of the archegonia, and the sporogonia are situated on the dorsal surface and are surrounded by a sheath-like outgrowth of the thallus forming a perichaetium. To this group belong the thalloid forms (*Pellia, Metzgeria*)

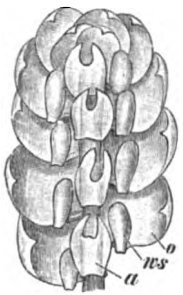


FIG. 450.—Part of a shoot of *Frullania Tamarisci*, seen from below. *o*, Dorsal leaves with the lower lobes (*ws*) modified as water-sacs; *a*, amphigastrium. (× 35.)

FIG. 451.—*Haplomitrium Hookeri*. *a*, Origin of a new shoot; *r*, rhizome; *o*, lower limit of the aerial shoot. (After GOTTSCHE.)

and others showing a transition to the foliose forms (*Blasia*). 2. In the **Akrogynae**, on the other hand, the archegonia and the sporogonium stand at the end of the main stem or of a branch and are surrounded by a perianth formed of modified leaves. To this group belong the dorsiventral leafy forms, *e.g. Plagiochila, Frullania*, and *Jungermannia*, a genus with numerous species. 3. The **Haplomitrieae** hold an isolated position, but appear to exhibit the closest connection with the Anakrogynae. This order contains only two genera, *Calobryum*, occurring in the tropics, and *Haplomitrium*. The single species of the latter genus, *H. Hookeri* (Fig. 451), occurs in Europe, and possibly is a survival of pre-glacial Liverworts. The Calobryaceae differ from all other Liverworts in the radial construction of their shoot, which bears three rows of leaves. The sexual organs form terminal groups in *Calobryum*, in *Haplomitrium* they occur between the upper leaves.

CLASS II

Musci (Mosses) (1, 92, 93, 104-110)

The Mosses include a large number of forms distributed in all parts of the world. They grow on dry soil, in swamps, on rocks, on tree-trunks and in tropical forests, also as epiphytes on the branches, and less commonly in water;

their structure is correspondingly various. Close tufts or masses are especially characteristic of dry habitats, while the typical inhabitants of the soil of woods have a looser mode of growth. In the moist mountain forests of the tropics and sub-tropics Mosses often grow in considerable masses surrounding the branches or hanging in long veil-like masses from them (105).

The Bog-Mosses form extensive growths on moors, as also do others (especially *Polytrichum*) on the moist soil in the arctic moss-tundras.

The profusely-branched protonema of the Mosses appears to the naked eye as a felted growth of fine, green filaments (Fig. 432).

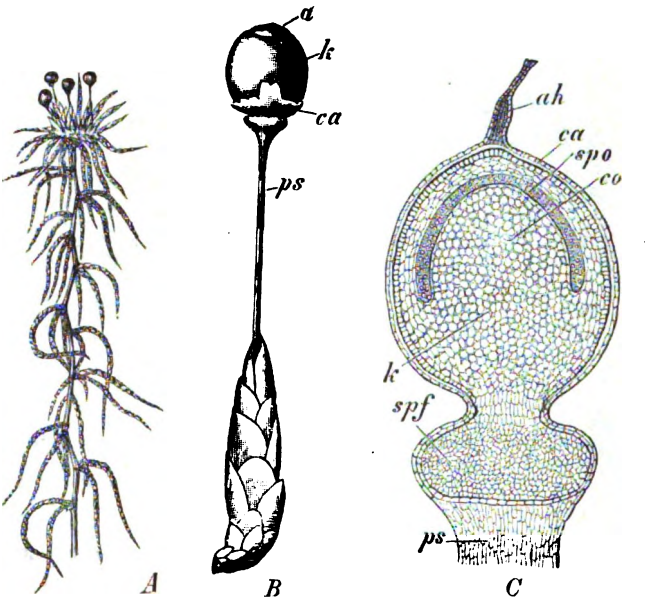


FIG. 452.—*Sphagnum fimbriatum: A*, A shoot with four ripe sporogonia. *Sphagnum squarrosum: B*, A lateral shoot with a terminal sporogonium; *ca*, ruptured calyptra; *d*, operculum. *Sphagnum acutifolium: C*, a young sporogonium in longitudinal section; *ps*, pseudopodium; *ca*, archegonial wall or calyptra; *ah*, neck of archegonium; *spf*, foot of sporogonium; *k*, capsule; *co*, columella; *spo*, spore-sac with spores. (*B* and *C* after W. P. SCHIMPER; *A*, nat. size; the other figures magnified.)

The oblique position of the cell walls in the filaments is characteristic. The young moss plants are developed on the protonema as small buds which arise as protrusions of cells of the filament, usually from the basal cell of one of the branches. The protrusion is cut off by a transverse septum, and after the separation of one or two stalk-cells the three-sided pyramidal apical cell of the moss plant is delimited in the enlarged terminal cell (106). The moss plants are always differentiated into stem and leaf. The Mosses may be readily distinguished from the foliose Jungermanniaceae by the spiral arrange-

ment of their small leaves, which are rarely arranged in two rows. In Mosses which have prostrate stems the leaves, although arranged spirally, frequently assume a somewhat outspread position, and all face one way, so that in such cases a distinction between an upper and a lower side is manifested, but in a manner different from that of the Liverworts.

The STEM OF THE MOSS PLANT is formed of cells which become gradually smaller and thicker-walled towards the periphery. In the stems of many genera (*e.g. Polytrichum*, *Mnium*, Fig. 96 and p. 82) there is found a central, axial strand consisting of elongated, conducting cells with narrow lumina. These strands are not as highly differentiated as the vascular bundles of Pteridophytes. They have neither vessels

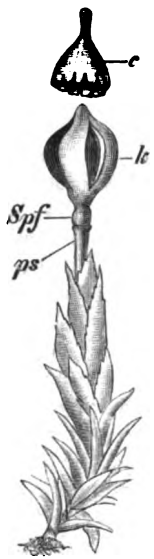


FIG. 453.—*Andreaea petrophila*. *ps*, Pseudopodium; *Spf*, foot; *k*, capsule; *c*, calyptra. (× 12.)

FIG. 454.—*Polytrichum commune*. *rh*, Rhizoids; *s*, seta; *c*, calyptra; *ap*, apophysis; *d*, operculum. (Nat. size.)

nor sieve-tubes, but serve for the conduction of water and organic substances. They are wanting in the Sphagnaceae or Bog Mosses which grow in swampy places. The stems of the Sphagnaceae show a peculiar development of the outer cortical layers. The cells in these layers are devoid of protoplasm, and are in communication with each other and the atmosphere by means of large, open pores; to secure rigidity, they are also provided with spirally-thickened walls.

They have a remarkable power of capillary absorption, and serve as reservoirs for storing and conducting water.

The LEAVES of the true Mosses have, as a rule, a very simple structure. They consist usually of a single layer of polygonal cells containing chloroplasts and are generally provided with a median conducting bundle of elongated cells. The leaves of the Bog Mosses (Sphagnaceae) have no bundles, and instead are supplied with capillary cells for the absorption and storage of water. These cells are devoid of protoplasm, and are similar to those in the periphery of the stem, but larger and more elongated; their walls, which are perforated, are strengthened by transverse thickening bands. Between them are other elongated, reticulately united cells containing chloroplasts. A similar differentiation of the leaf-cells occurs in a few other Mosses (*e.g. Leucobryum glaucum*).

A more complicated structure of the leaves resulting from their adaptation to the absorption of water and protection against drying is exhibited by *Polytrichum commune*. In this Moss the leaves develop on their upper surface numerous, crowded, vertical lamellae, one cell thick; these contain chlorophyll and serve as an assimilatory tissue, while the spaces between the lamellae serve as reservoirs for the storage of water. In a dry atmosphere the leaves fold together, and thus protect the delicate lamellae from excessive transpiration ([107]). Many Mosses can endure desiccation without injury.

The RHIZOIDS (Figs. 454, 456), each of which consists of a branched filament of cells without chlorophyll, spring from the base of the stem. In structure they resemble the protonema, into which they sometimes become converted, and then can give rise to new moss plants.

The SEXUAL ORGANS are always borne in groups at the apices either of the main axes or of small, lateral branches, surrounded by the upper leaves of the latter which frequently have a distinctive structure, and are known as the PERICHAETIUM (Fig. 456). Between the sexual organs there are usually present a number of multicellular hairs or paraphyses. The moss plants may be monoecious, in which case both kinds of sexual organs are borne on the same plant either in the same or different receptacles; or dioecious, and then the antheridia and archegonia arise on different plants. The archegonia and antheridia of Mosses differ in their development from those of other Archegoniatae by being formed by the segmentation of a two- or three-sided apical cell.

The SPOROGONIUM of the Mosses ([108]) develops a capsule with an axial COLUMELLA consisting of sterile tissue (Fig. 458). The spore-sac surrounds the columella, which conducts and accumulates food material and water for the developing spores. Elaters are never formed. In the young sporogonium outside the spore-sac a well-developed assimilating tissue is present; this is bounded by water-storage tissue and an epidermis. In most Mosses stomata are found on the lower part of the capsule. The ripe capsule exhibits a variety of peculiar structures to facilitate the opening and the distribution of the spores. The stalk or seta raises the capsules so that the spores are readily dispersed by wind. Distinctive variations in the mode of development and structure of the capsules are exhibited by the three orders of the Musci: *Sphagnales*, *Andreaeales*, and *Bryales*.

Order 1. Sphagnales (109)

The Sphagnaceae, or Bog Mosses, are the only family and include only a single genus, *Sphagnum*, containing many species. The Bog Mosses grow in swampy places, and form large tussocks saturated with water. The upper extremities of the stems continue their growth from year to year, while the lower portions die away and become eventually converted into peat. Of the numerous lateral branches arising from each of the shoots, some grow upwards and form the apical tufts or heads at the summits of the stems; others, which are more elongated and flagelliform in shape, turn downwards and envelop the lower portions of the stem (Fig. 452 *A*). Every year one branch below the apex develops as strongly as the mother shoot, so that the stem becomes falsely bifurcated. By the gradual death of the stem from below upwards the daughter shoots become separated from it, and form

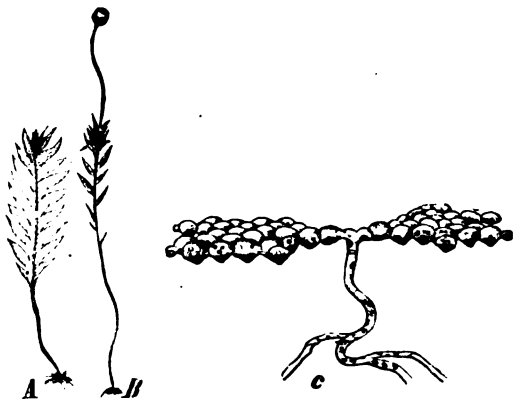


FIG. 455.—*Schistostega osmundacea*. *A*, Sterile; *B*, fertile plant. (× 5.) *C*, Protonema. (× 90. After NOLL.)

FIG. 456.—*Mnium undulatum*. Orthotropous shoot terminating in a male receptacle surrounded by involucral leaves. The lateral shoots are plagiotropous. (After GOEBEL.)

FIG. 457.—*Scleropodium purum*. (Nat. size.)

independent plants. Special branches of the tufted heads are distinguishable by their different structure and colour; on these the sexual organs are produced. The male branches give rise, near the leaves, to spherical stalked antheridia. The archegonia are borne at the tips of the female branches. The sporogonium develops a short stalk with an expanded foot (*B*, *C*), but remains for a time enclosed by the archegonial wall or calyptra. Upon the rupture of the archegonium, the calyptra persists, as in the Hepaticae, at the base of the sporogonium. The capsule is spherical and has a dome-shaped columella, which in turn is overarched by a hemispherical spore-sac (*spo*); it opens by the removal of an operculum. The ripe sporogonium is borne upon a prolongation of the stem axis, the pseudopodium, which is expanded at the top to receive the foot of the stalk. Of the peculiar structure of the leaves and stem cortex a description has already been given above. The protonema of the Sphagnaceae is in some respects peculiar. Only a short filament is formed on the germination of the spore, the protonema broadening out almost at once into a flat structure on which the young moss plants arise.

Order 2. Andreaeales

The Andreaeales comprise only the one genus, *Andreaea*, small, brownish, caespitose Mosses growing on rocks. The sporogonium is also terminal in this order. The capsule, at first provided with a calyptra, splits into four longitudinal valves (schizocarpous), which remain united at the base and apex (Fig. 453). The stalk is short, and is expanded at the base into a foot (*Spf*), which in turn is borne, as in *Sphagnum*, on a pseudopodium (*ps*), a stalk-like prolongation of the stem resulting from its elongation after the fertilisation of the archegonium. The protonema is ribbon-shaped.

Order 3. Bryales [110]

In this order, which includes the great majority of all the true Mosses, the moss fruit attains its most complicated structure. The ripe SPOROGONIUM, developed from the fertilised egg, consists of a long stalk, the SETA (Fig. 454 *s*), with a FOOT at its base, sunk in the tissue of the mother plant, and of a CAPSULE, which in its young stages is surmounted by a hood or CALYPTRA. The calyptra is thrown off before the spores are ripe. It consists of one or two layers of elongated cells, and originally formed part of the wall of the archegonium; this, at first, enclosed the embryo, growing in size as it grew, until, finally ruptured by the elongation of the seta, it was carried up as a cap, covering the capsule. It consists of several layers of cells and, especially in forms which occupy dry habitats, bears hairs that correspond to protonemal threads of limited growth. In some Mosses (*e.g. Funaria*) the young calyptra is distended and serves as a reservoir of water for the young sporogonium [111]. The upper part of the seta, where it joins the capsule, is termed the APOPHYSIS. In *Mnium* (Fig. 460 *A*, *ap*) it is scarcely distinguishable, but in *Polytrichum commune* it has the form of a swollen ring-like protuberance (Fig. 454 *ap*), while in species of *Splachnum* it dilates into a large collar-like structure of a yellow or red colour. The upper part of the capsule becomes converted into a lid or operculum which is sometimes drawn out into a projecting tip. At the margin of the operculum a narrow zone of epidermal cells termed the ring or ANNULUS becomes specially differentiated. The cells of the annulus contain mucilage, and by their expansion at maturity assist in throwing off the lid. In most Mosses the mouth of the dehisced capsule bears

a fringe, the PERISTOME, consisting usually of tooth-like appendages, but in others this is wanting.

The peristome of *Mnium hornum* (Fig. 460), which will serve as an example, is double; the outer peristome is formed of 16 pointed, transversely striped teeth inserted on the inner margin of the wall of the capsule. The inner peristome lies just within the outer, and consists of cilia-like appendages, which are ribbed on the inner side and thus appear transversely striped; they coalesce at their base into

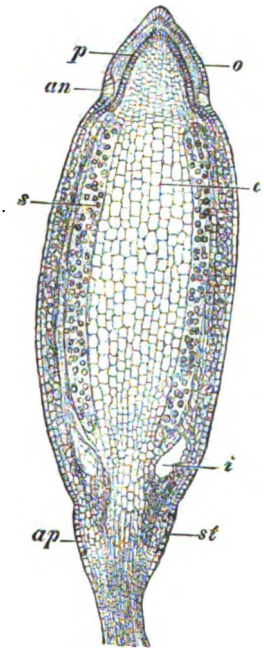


FIG. 458.—*Mnium hornum*. Median longitudinal section of a half-ripe sporogonium. *o*, Operculum; *p*, peristome; *c*, columella; *s*, spore-sac containing the spores; *i*, air-space; *ap*, apophysis; *st*, stomata. (× 18. After STRASBURGER.)

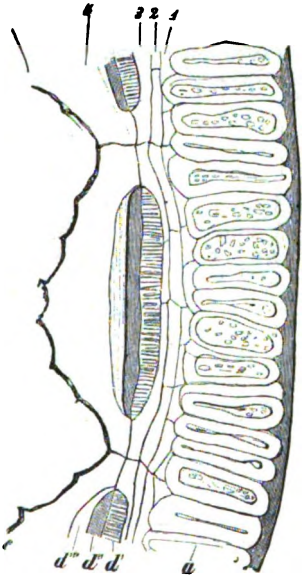


FIG. 459.—*Mnium hornum*. Transverse section through the wall of the capsule in the region of the ring. *a*, Cells of the ring; *1-4*, successive cell layers with the thickened masses of the peristome, *d'*, *d''*; *d'''*, transverse projecting ribs; *c*, the coalesced cilia. (× 240. After STRASBURGER.)

a continuous membrane. Two cilia of the inner peristome are always situated between each two teeth of the outer row.

The teeth and cilia of the peristome are formed in this instance of thickened portions of the opposite walls of a single layer of cells next to the operculum (Fig. 459), the teeth from portions of the external wall, and the cilia from portions of the internal walls of the same layer. On the opening of the capsule the unthickened portions of this layer break away and the teeth and cilia split apart. The transversely-ribbed markings on their surface indicate the position of the former transverse walls.

In the Polytrichaceae the origin of the peristome teeth follows a peculiar type; they are composed of a number of elongated entire cells.

The structure of the peristome varies greatly within the Bryales. By its

peculiar form and hygroscopic movements the peristome causes a gradual dissemination of the spores from the capsule.

Variations in the form of the capsule, peristome, operculum, and calyptra afford the most important means of distinguishing the different genera. The Bryales are divided into two sub-orders, according to the position of the archegonia or of the sporogonia developed from them.

(*a*) In the **Acrocarpi** the archegonia, and consequently the sporogonia, are terminal on the main axis. *Mnium undulatum* (Fig. 456) and *hornum*, *Polytrichum commune* (Fig. 454), and *Funaria hygrometrica* are common examples. *Schistostega osmundacea*, a moss living in caves, has fertile shoots, which have spirally-arranged leaves and bear stalked capsules devoid of peristomes, and also other shoots that are sterile, with two rows of leaves (Fig. 455). The protonema of this species is peculiarly constructed and gives out an emerald phosphorescent

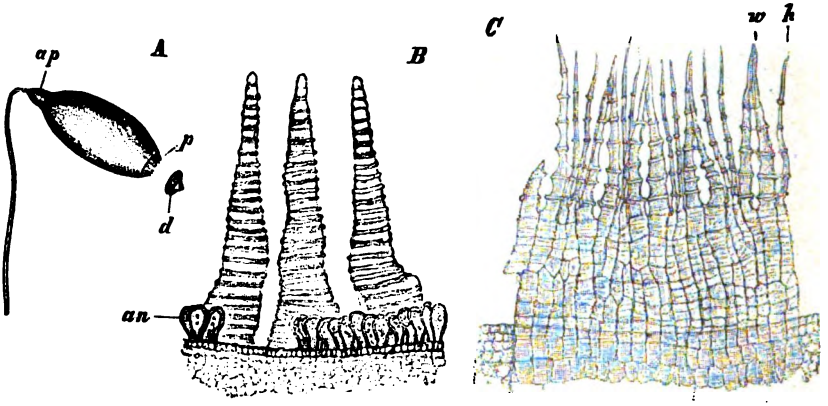


FIG. 460.—*Mnium hornum*. *A*, Capsule with upper portion of seta; *ap*, apophysis; *p*, peristome; *d*, the separated operculum. *B*, Three teeth of the outer peristome seen from the outside; *an*, annulus. *C*, Inner peristome seen from the inside; *w*, broader cilia; *h*, narrower cilia. (*A* × 4; *B*, *C* × 60.)

light. In some minute Mosses (*Archidium*, *Phascum*, *Pleuridium*) the sporogonium is considerably simplified, the formation of operculum, annulus, and peristome being suppressed and the spores set free by decay of the capsule.

(*b*) In the **Pleurocarpi** the growth of the main axis is unlimited, and the archegonia with their sporogonia arise on short, lateral branches (Fig. 457). In this group are included numerous, usually profusely-branched species of large Mosses belonging to the families Neckeraceae and Hypnaceae, which are among the most conspicuous mosses of our woods, and also the submerged Water Moss, *Fontinalis antipyretica*.

III. PTERIDOPHYTA (VASCULAR CRYPTOGAMS) ([1, 92, 112-181])

The Pteridophytes include the Ferns, Water-Ferns, Horse-tails, and Club Mosses, and represent the most highly developed Cryptogams. In the development of the plants forming this group, as in the Bryophyta, a distinct alternation of generations is exhibited. The

sexual generation bears the antheridia and archegonia; the asexual generation develops from the fertilised egg and produces asexual, unicellular spores. On germination the spores in turn give rise to a sexual generation. Since the reduction division takes place on the formation of the spores, the sexual generation is haploid and the asexual generation diploid.

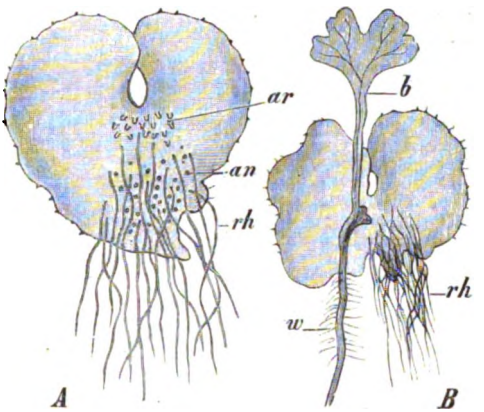


FIG. 461.—*Dryopteris* (*Aspidium*) *filix mas*. *A*, Prothallium seen from below; *ar*, archegonia; *an*, antheridia; *rh*, rhizoids. *B*, Prothallium with young fern attached to it by its foot; *b*, the first leaf; *w*, the primary root. (× circa 8.)

The SEXUAL GENERATION is termed the PROTHALLIUM or GAMETOPHYTE. It never reaches any great size, being at most a few centimetres in diameter; in some forms it resembles in appearance a simple, thalloid Liverwort; it then consists of a small green thallus, attached to the soil by rhizoids springing from the under side (Fig. 461 *A*). In other cases the prothallium is branched and filamentous; sometimes it is a tuberous, colourless mass of tissue, partially or wholly buried in the ground, and leading a saprophytic existence, in symbiosis with an endophytic fungus forming a mycorrhiza, while in certain other divisions of the Pteridophyta it undergoes reduction and remains more or less completely enclosed within the spore. On the prothallia arise the sexual organs, antheridia (Figs. 468, 475), producing numerous ciliate, usually spiral spermatozoids, and archegonia (Figs. 469, 476), in each of which is a single egg-cell. As in the Mosses the presence of water is necessary

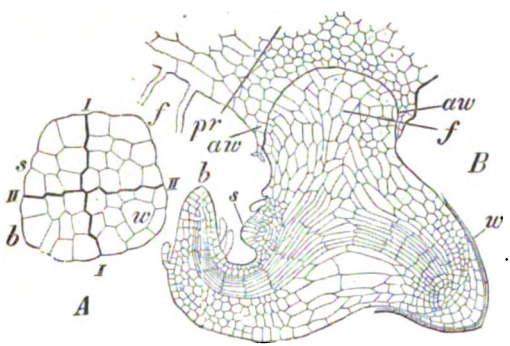


FIG. 462.—*A*, *Pteris serrulata*, embryo freed from the archegonium, in longitudinal section (after KIENITZ-GERLOFF): *I*, basal wall; *II*, transverse wall dividing the egg-cell into quadrants; rudiment of the foot *f*, of the stem *s*, of the first leaf *b*, of the root *w*. *B*, Section of a further-developed embryo of *Pteridium aquilinum* (after HOFMEISTER); *f*, foot still embedded in the enlarged venter of the archegonium *aw*; *pr*, prothallium. (Magnified.)

for fertilisation. The spermatozoids are induced to direct their motion toward the archegonia by the excretion from the latter of a substance which diffuses into the surrounding water. In Ferns, *Salvinia*, *Equisetum*, *Selaginella*, and *Isoetes*, this substance is malic acid or one of its salts, while in *Lycopodium* it is citric acid.

Other organic acids, some salts of the metals, and even some alkaloids may serve as attractive substances. Differences exist in the behaviour of different genera in this respect. The chemotactic sensibility of the spermatozoids may exist for a number of substances ([113]).

After the fertilisation of the egg-cell by a spermatozoid there is developed from it, as in the Bryophyta, the diploid asexual generation; this is the cormophytic fern-plant.

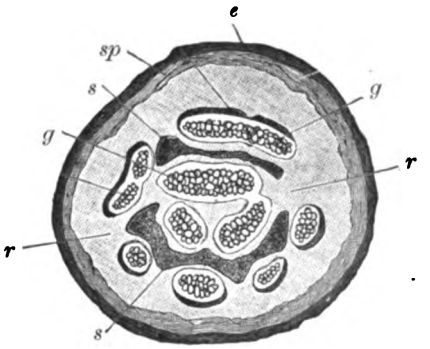


FIG. 468.—Transverse section of the rhizome of *Pteridium aquilinum*. *g*, Concentric vascular bundles; *s*, sclerenchymatous plates; *sp*, peripheral zone of sclerenchymatous fibres; *r*, cortex; *e*, epidermis. (× 7.)

The asexual generation or sporophyte is represented by a plant possessing a highly differentiated internal structure, and externally segmented into stem, leaves, and roots. In the majority of Pteridophytes (Ferns, *Equisetum*), the fertilised egg-cell, while still in the archegonium, surrounds itself with a cell wall and undergoes division, first into two cells, by the formation of a basal wall, and then into octants by two walls at right angles to each other and to the basal wall. By the further division of these eight cells a small mass of tissue is formed, and from this are developed the stem apex, the first leaf, the primary root, and an organ peculiar to the Pteridophytes, the so-called FOOT (Fig. 462 *f*). The foot is a mass of tissue, by means of which the young embryo remains attached to the parent prothallium and absorbs nourishment from it, until, by the development of its own roots and leaves, it is able to nourish itself independently. In some Lycopodineae (*Lycopodium*, *Selaginella*) a suspensor consisting of one or a few cells is formed and serves as an absorbent organ. The prothallium usually dies after the development of the young plant. The stem developed from the embryonic rudiment may be either simple or bifurcated, erect or prostrate; it branches without reference to the leaves, which are arranged spirally or in whorls, or occupy a dorsiventral position. Instead of rhizoids, as in the Bryophyta, true roots are produced, as in the Phanerogams. The

leaves also correspond in structure with those of the Phanerogams. The three primary organs in most Pteridophyta grow by means of apical cells (Figs. 100, 101, 156). Such apical cells are not to be recognised in *Lycopodium* and *Isoetes*, while *Selaginella* shows both growth by an apical cell and the transition to growth by a number of initial cells. Stems, leaves, and roots are traversed by well-differentiated vascular bundles, and the Pteridophytes are, in consequence, designated Vascular Cryptogams. The bundles of the great majority of Pteridophytes are as a rule constructed on the concentric and radial types (cf. pp. 99 ff., Figs. 463, 464). Secondary growth in thickness, resulting from the activity of a special cambium, occurs only

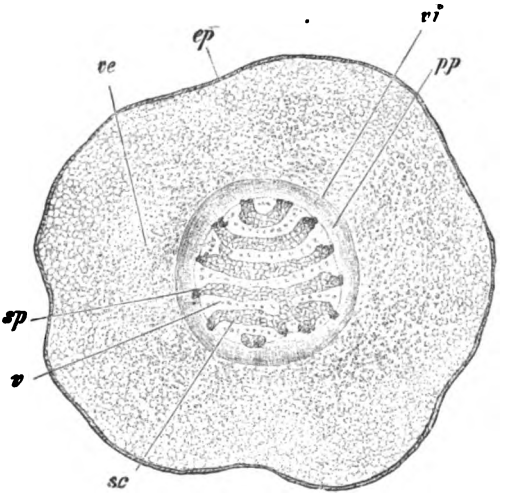


FIG. 464.—Transverse section of stem of *Lycopodium complanatum*. *ep*, Epidermis; *ve*, *vi*, *pp*, outer, inner, and innermost parts of the primary cortex, surrounding the central cylinder composed of xylem and phloem regions; *sc*, scalariform tracheides; *sp*, annular and spiral tracheides; *v*, phloem. (× 26. After STRASBURGER.)

occasionally in existing forms, but it was characteristic of the stems of certain extinct groups of Pteridophytes.

The course of the vascular bundles in the leaves (venation) provides important characters for classification, especially in the Ferns (Fig. 465). While only a single median nerve is present in the simple leaves of the Horse-tails and Club-mosses the nerves of the leaves of Ferns branch in the most various fashion; they may be dichotomous or pinnate and either end freely or anastomose to form a system of meshes. In these polygonal meshes the ultimate branches may end blindly.

The SPORES are produced in special receptacles termed SPORANGIA (Fig. 466), which occur on the asexual generation, either on the leaves, or less frequently on the stems in the axils of the leaves. The leaves which bear the sporangia are termed SPOROPHYLLS. The

sporangium consists of a wall enclosing the sporogenous tissue, the cells of which, becoming rounded off and separated from each other as spore-mother-cells, give rise each by a reduction division to four tetrahedral spores (spore-tetrads). The cells of the innermost layer of the sporangial wall are rich in protoplasm, and constitute the TAPETUM. This layer persists in the Lycopodineae, but in the case of the Ferns and Equisetineae the walls of the tapetal layer become dissolved. In the course of the development of the sporangium the tapetal cells then wander in between the spore-mother-cells, their nuclei dividing amitotically, so that the spores eventually lie embedded in a mucilaginous protoplasmic mass, the PERIPLASM, from which they derive nourishment (114). The wall of the mature sporangium is formed of one or a number of layers of cells. The unicellular spores have cell walls composed of several layers. The young spore on becoming isolated in the tetrad surrounds itself with a cutinised membrane (exospore) within which a cellulose layer (endospore) is deposited. In many cases a perispore is deposited

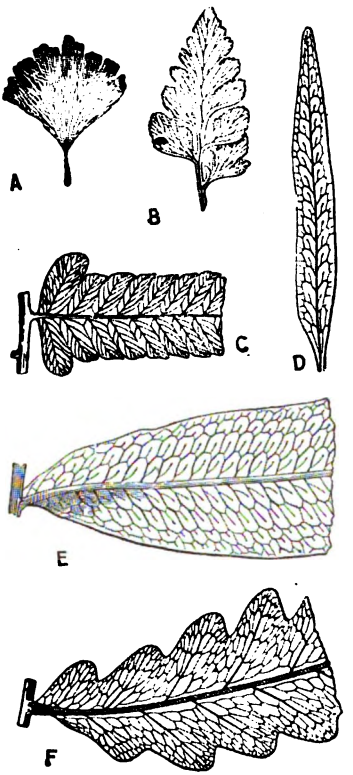


FIG. 465.—Venation of Ferns. *A*, *Adiantum capillus veneris* (venatio cyclopteridis). *B*, *Asplenium adiantum nigrum* (v. sphenopteridis). *C*, *Asplenium esculentum* (v. goniopteridis). *D*, *Polypodium serpens* (v. marginariae). *E*, *Polypodium nereifolium* (v. goniophlebii). *F*, *Onoclea sensibilis* (v. sageniae).

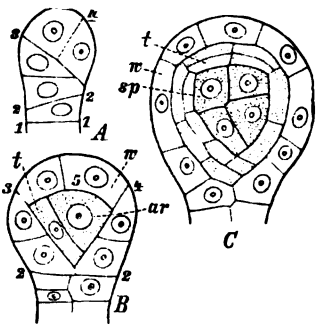


FIG. 466. — Development of the sporangium of *Asplenium*. *A*, First divisions of the young sporangium which has originated from a single superficial cell. *B*, Division into the wall (*w*), and the central archesporial cell (*ar*) which has cut off one of the tapetal cells (*t*). *C*, Older stage in which the archesporial cell has given rise to the tapetal cells and the sporogenous tissue (*sp*). (× 300. After SADEBECK.)

by the periplasm upon the exospore (in Horse-tails, Hydropterideae, and some Ferns).

The spores of the majority of the Pteridophytes are of one kind, and give rise on germination to a prothallium, which produces both antheridia and archegonia. In certain cases, however, the prothallia are dioecious. This separation of the sexes extends in some groups even to the spores, which, as MACROSPORES (megaspores), developed in MACROSPORANGIA (megasporangia), give rise only to female prothallia; or as MICROSPORES, which are produced in MICROSPORANGIA, develop similarly only male prothallia. In accordance with this difference in the spores, a distinction may be made between the HOMOSPOROUS and HETEROSPOROUS forms of the same group; but this distinction has no systematic value in defining the different groups themselves, as it has arisen independently in several of them.

The correspondence in the structure of their antheridia, archegonia, and spore-mother-cells is in favour of a relationship between the Bryophyta and the Pteridophyta. Though both groups may have had their origin from a common group of Algae (p. 482), an independence in the further course of development must be assumed in the two cases. In particular, it is impossible to derive the sporophyte of the Pteridophyta from the sporophyte or sporogonium of the Moss. While the latter without attaining any vegetative complexity comes to an end early with spore-formation, the Fern sporophyte becomes differentiated into stem, leaf, and root. The vascular bundles appear as quite new structures, the possession of which enables the sporophyte to proceed to the development of a large complicated and sometimes tree-like terrestrial plant; this contrasts with the Bryophyta, where, owing to the simple cellular structure and the absence of special water-conducting channels, no great size can be reached. The plant only proceeds at a late stage to the production of spores. The spore-mother-cells are formed endogenously in special parts of the leaf; these are indeed called "sporangia," but are not homologous with the sporangia of Thallophyta. On this account it would seem advisable to use a new term (sporothecae) for the so-called sporangia of Pteridophyta. The spore-mother-cells, which may be most closely compared with the tetrasporangia of Brown and Red Algae, correspond, rather than the sporothecae, to the sporangia of Thallophyta.

The gametophyte of the Vascular Cryptogams closes its development early by the formation of sexual organs. The typical fern-prothallus hardly surpasses the juvenile form of a thallus, while in the Bryophyta, on the other hand, the sexual generation exhibits a progressive development (98).

The Pteridophyta are divided into the following Classes.*

1. *Filicinae.*—Ferns. Stem simple or branched, with well-developed, alternate, often deeply-divided or compound leaves called

[* To these must be added the recently established Class of the Psilophytales. This includes the most simply organised Vascular Cryptogams. In some (*Rhynia, Hornea*) the plant is rootless and leafless, consisting of a rhizome, branched cylindrical aerial stems, and large terminal sporangia. In *Asteroxylon* and *Psilophyton* the stems bear small simple leaves. A full account of these simple Vascular Cryptogams of Early Devonian age will be found in Scott's *Studies in Fossil Botany*, 3rd ed., vol. i.]

fronds. Sporangia either on the under side of the sporophylls, united in sori or free, or enclosed in special segments of the leaves. Spermatozoids multiciliate.

Sub-Class 1. *Filicinae eusporangiatae.*—Ripe sporangia with firm wall composed of several layers of cells. Homosporous.

Sub-Class 2. *Filicinae leptosporangiatae.*—Ripe sporangia with walls one layer thick.

Order 1. *Filices.*—Ferns, in the narrower sense. Homosporous.

Order 2. *Hydropterideae.*—Water-Ferns. Heterosporous.

2. *Equisetinae.*—Horse-tails. Stem simple or verticillately branched, with whorled, scale-like leaves forming a united sheath at each node. Sporophylls peltate, bearing a number of sporangia on the under side, and aggregated into a cone at the apex of each fertile shoot. Spermatozoids multiciliate.

Order 1. *Equisetaceae.*—Horse-tails. Homosporous, herbaceous plants.

Order 2. *Calamariaceae.*—Calamites. Homosporous or heterosporous. Extinct arborescent plants.

3. *Sphenophyllinae*

Order 1. *Sphenophyllaceae.*—Stem slender; leaves in whorls. Sporophylls with 1–4 sporangia, borne in cones. Homosporous. Extinct plants.

4. *Lycopodinae.*—Stem simple or dichotomously branched. Roots dichotomous. Leaves alternate, simple. Sporangia with firm walls, always borne singly in the axils of the sporophylls.

Order 1. *Lycopodiaceae.*—Club-mosses. Homosporous; spermatozoids biciliate; herbs with dichotomously branched shoots.

Order 2. *Psilotaceae.*—Homosporous; stem herbaceous, dichotomously branched, with alternate, simple, or scale-like leaves; rhizomes in place of roots; sporophylls forked, each bearing on the adaxial face close to its base a 2- or 3-locular sporangium.

Order 3. *Selaginellaceae.*—Heterosporous; spermatozoids biciliate; herbs with dichotomous stems and small leaves.

Order 4. *Isoetaceae.*—Quill-worts. Heterosporous; spermatozoids multiciliate; stem tuberous, simple, with secondary thickening; leaves awl-shaped.

Order 5. *Sigillariaceae.*—Extinct. Heterosporous; arborescent; stem simple or sparingly branched dichotomously.

Order 6. *Lepidodendraceae.* — Extinct. Heterosporous; repeatedly dichotomously branched trees.

5. *Pteridospermeae.*—Extinct plants with the habit of large ferns. Heterosporous with microsporangia and seed-like macrosporangia. Derived from Eusporangiate Ferns.

CLASS I

Filicinae (Ferns) ([1, 92, 112, 115])

The great majority of existing Pteridophytes belong to the Ferns, taking the group in a wide sense. Two sub-classes are distinguished according to the structure of the sporangia. The Eusporangiate Ferns are characterised by sporangia, the thick wall of which consists of a number of layers of cells. They open by a longitudinal split. The Leptosporangiate Ferns, on the other hand, have sporangia which, when mature, have their wall formed of one layer of cells, and dehisce transversely or longitudinally. Stipules, which are found at the base of the frond in the former group, are wanting in the Leptosporangiatae. Differences also exist in the prothallus and in the structure of the sexual organs. Only in some groups of Leptosporangiatae is there a perispore deposited on the outside of the exospore.

While in earlier geological periods the Eusporangiatae were abundantly represented, they now include only two families, each with a few genera. They appear to represent the more ancient type of Ferns and to stand nearest to the forms from which the Filicinae have been derived. Along with them, even in palaeozoic times we have the Leptosporangiatae, from which in later cretaceous and tertiary times the Hydropterideae have branched off as a small group of aquatic or marsh-growing Ferns. In the Hydropterideae only among Ferns the spores are differentiated into microspores and macrospores.

Sub-Class I. Eusporangiatae

Order 1. Marattiaceae ([116])

This order, perhaps the most primitive of existing Ferns, includes about 20 stately tropical ferns with thickened tuberous stems and usually very large leaves provided with two stipules at the base. The sporangia are situated in groups (sori) on the under surface of the leaves, and are either free (*Angiopteris*) or united to form an oval capsule-like body, the chambers of which are the sporangia. The prothallium in contrast to that of the Ophioglossaceae is a green, heart-shaped thallus, resembling that of a Liverwort and growing on the surface of the soil. It is sometimes dichotomously branched. The sexual organs resemble those of the following order but are developed on the lower surface of the prothallus. An endophytic fungus occurs in the cells of the prothallus.

Order 2. Ophioglossaceae [117]

European examples of this order, which contains only a few species, are afforded by *Ophioglossum vulgatum*, Adder's Tongue (Fig. 467 *E*), and *Botrychium*, Moonwort (Fig. 467 *A*). Both have a short stem, from which only a single leaf unfolds

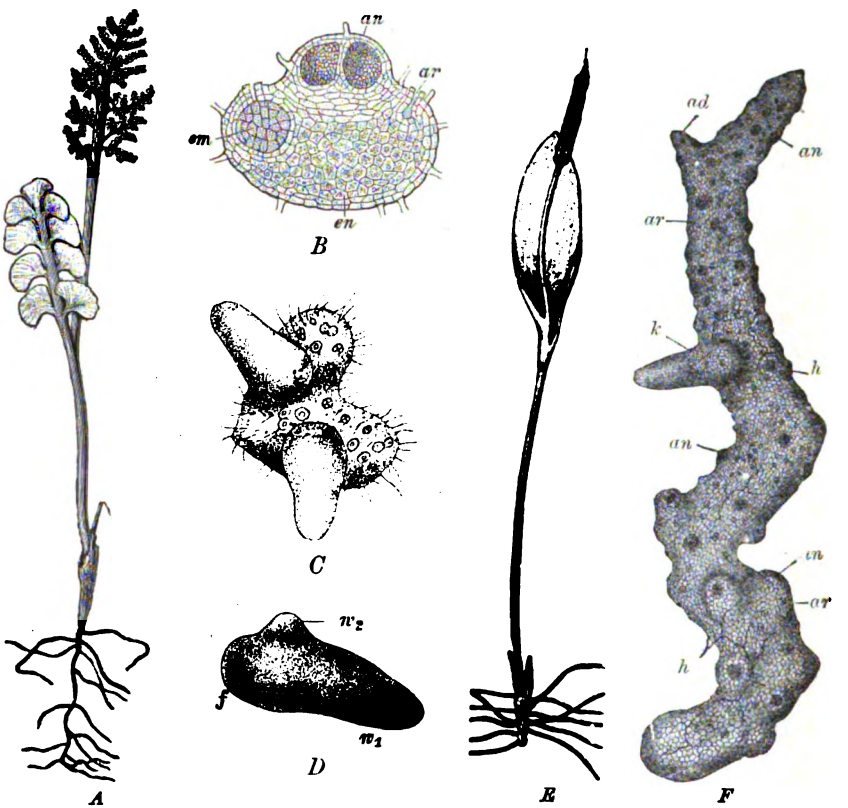


FIG. 467.—*A*, *Botrychium lunaria*. Sporophyte. ($\frac{1}{2}$ nat. size.) *B*, Transverse section of the prothallus; *an*, antheridium; *ar*, archegonium; *em*, embryo; *en*, fungal hyphae (× 45). *C*, Prothallus bearing two embryos, the roots of which have emerged (× 16). *D*, Embryo with the first and second roots (w_1, w_2) and foot (*f*) (× 16). *E*, *Ophioglossum vulgatum*. Sporophyte showing the bud for the succeeding year. ($\frac{1}{2}$ nat. size.) *F*, *Ophioglossum vulgatum*. Prothallus. *an*, antheridia; *ar*, archegonia; *k*, young plant with the first root; *ad*, adventitious branch; *h*, fungal hyphae. (× 15. *B-D*, *F* after BRUCHMANN.)

each year. The leaves in both cases are provided with leaf-sheaths. In *Ophioglossum* the leaf is tongue-shaped, in *Botrychium* it is pinnate. These leaves bear on their upper side a fertile segment arising near the upper end of the leaf-stalk. This fertile segment in *Ophioglossum* is simple and cylindrical, with the sporangia sunk in two rows; in *Botrychium* it is pinnately branched in the upper part, and

thickly beset on the inner side with large, nearly spherical sporangia. The course of the vascular bundles and occasional reversions indicate that the fertile segment is derived from the union of two basal pinnae.

Our knowledge of the peculiar monoecious prothalli of the Ophioglossaceae is largely due to BRUCHMANN; they are long-lived, subterranean, saprophytic, tuberous bodies without chlorophyll but inhabited by a mycorrhizal fungus. In *Ophioglossum* (Fig. 467 *F*) they are cylindrical and radially symmetrical, simple or branched; in *Botrychium* (Fig. 467 *B*, *C*) they are oval or heart-shaped and dorsiventral. The antheridia (Fig. 468) and archegonia (Fig. 469) are sunk in the tissue of the prothallus. The antheridium encloses a large spherical mass of spermatozoid mother-cells which are set free when mature by the swelling of the

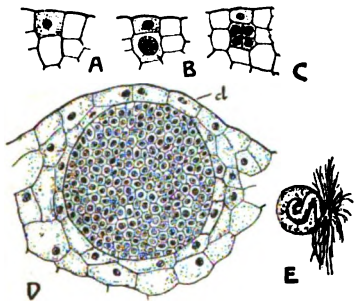


FIG. 468.—*Ophioglossum vulgatum*. *A-C*, Stages in the development of the antheridium from a superficial cell; the upper cell in *C* gives rise to the cover-cells, the lower to the mother cells of the spermatozoids. *D*, Antheridium not yet opened; *d*, cover-cells. *E*, Spermatozoid. (After BRUCHMANN.)

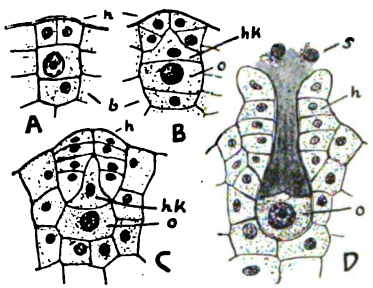


FIG. 469.—*Ophioglossum vulgatum*. *A-C*, Development of archegonium. *D*, Mature opened archegonium with two spermatozoids (*s*) in front of the opening; *h*, neck-cells; *hk*, neck-canal-cells; *o*, egg-cell; *b*, basal cell. (After BRUCHMANN.)

contents and the breaking down of one of the central cells of the outer wall. The spermatozoids have a spirally wound body and numerous cilia; a small vesicle is adherent to the spermatozoid (Fig. 468 *E*). The antheridia originate from single superficial cells (Fig. 468 *A-C*), as do also the archegonia (Fig. 469 *A-C*). The slightly projecting neck of the latter opens after the neck canal-cell has swollen and disintegrated; the oosphere (*o*) remains in the sunken venter. In many species the embryo leads a subterranean existence for several years. The primary root is first formed and soon projects from the archegonium (Fig. 467 *C*, *F*, *k*); later the first leaf and the apical cell of the stem are differentiated. In some species of *Botrychium* the embryo forms an elongated multicellular suspensor at the end of which the proper embryonic mass is formed. In this an agreement with the Lycopodinae is evident (cf. Fig. 493 and Fig. 498), which do not in other respects show any close relationship to the Eusporangiatae.

Sub-Class II. Leptosporangiatae

Order 1. Filices

The Filices, or Ferns, in the narrower sense of the word, comprise a large number of genera with numerous species, being widely distri-

buted in all parts of the world. They attain their highest development in the tropics. The Tree-Ferns (*Cyathea*, *Alsophila*, *Dicksonia*), which include the largest representatives of the order, occur in tropical countries, and characterise the special family of the Cyatheaceae. The stem of a Tree-Fern (Fig. 470) is woody and unbranched: it bears at the apex a rosette of pinnately-compound leaves or fronds, which are

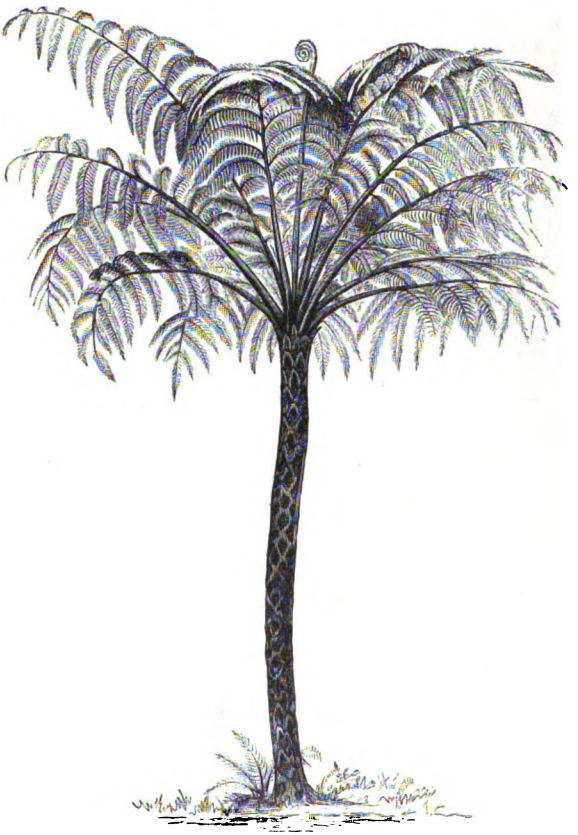


FIG. 470.—*Alsophila crinita*. A Tree-Fern growing in Ceylon. (Reduced.)

produced in succession from the terminal bud, and leave, when dead, a large leaf scar on the trunk. The stem is attached to the soil by means of numerous adventitious roots. The majority of ferns, however, are herbaceous, and possess a creeping rhizome, terminating usually in a rosette of pinnate or deeply-divided leaves. Such a habit and growth are illustrated by the common Male Fern *Dryopteris* (*Aspidium*) *filix mas*, the rhizome of which is official (Fig. 471). The

leaves of *Polypodium vulgare* are pinnate, and spring singly from

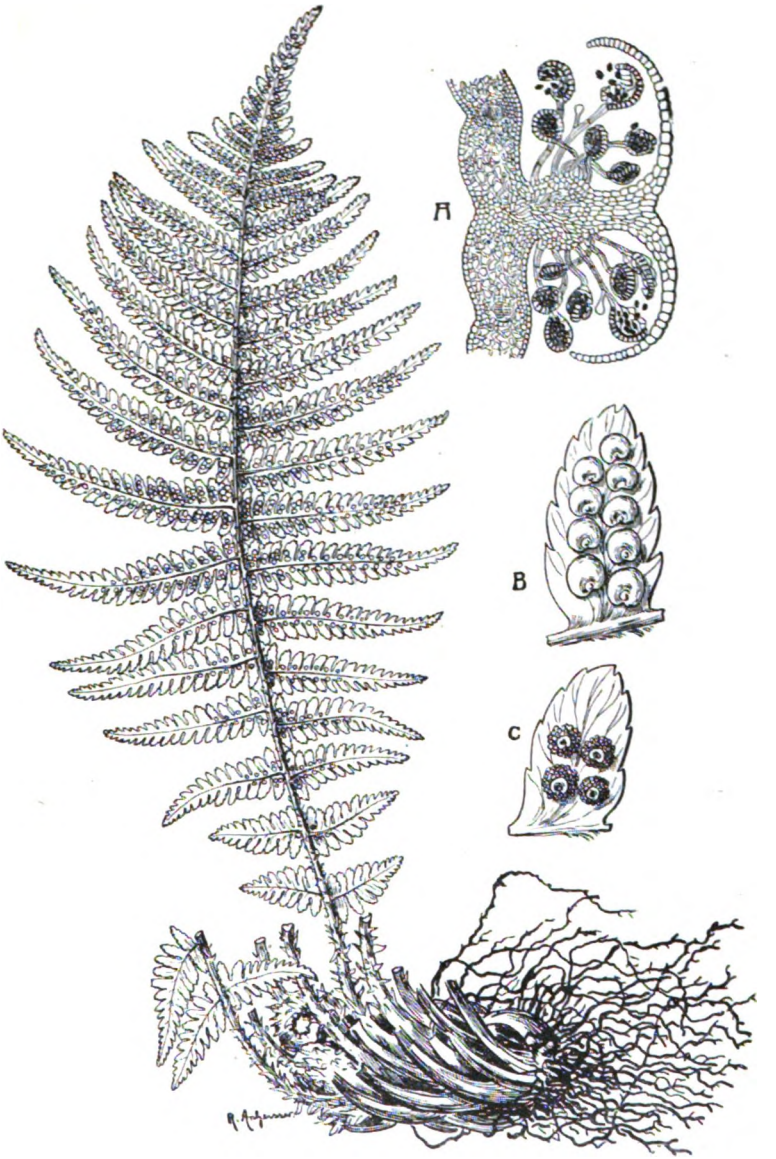


FIG. 471.—*Dryopteris* (*Aspidium*) *filix mas* (⅓ nat. size). *A*, Sorus in vertical section. (× 20. After KNY.) *B*, Pinna with young sori still covered by the indusia. *C*, Somewhat older sori with withered indusia. (Slightly magnified.) *OFFICIAL.*

the upper side of the creeping branched rhizome. In other cases the leaves may be simple and undivided, as in the Hart's-Tongue Fern, *Scolopendrium vulgare* (Fig. 472). In the tropics many herbaceous Ferns grow as epiphytes on forest trees (cf. p. 183). When young, the leaves are coiled at the tips (Fig. 470), a peculiarity common to the Ferns as a whole, and to the Water-Ferns. Unlike the leaves of most Phanerogams, those of the Ferns continue to grow at the apex until their full size is attained. Peculiar brownish scales (paleae, ramenta), often fringed and consisting of a single layer of cells, invest the stems, petioles, and sometimes also the leaves of most Ferns.

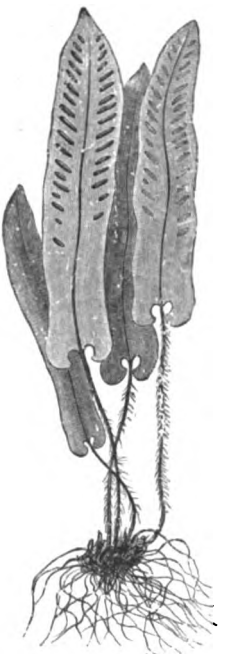


FIG. 472.—*Scolopendrium vulgare*. (¼ nat. size.)

The sporangia are generally produced in large numbers, on the under side of the leaves. The sporophylls, as a rule, resemble the sterile, foliage leaves. In a few genera a pronounced heterophylly is exhibited: thus in the Ostrich Fern, *Struthiopteris germanica*, the dark brown sporophylls are smaller and less profusely branched, standing in groups in the centre of a rosette of large foliage leaves. *Blechnum spicant* is another example.

In the different families, differences in the mode of development as well as in the form, position, and structure of the SPORANGIA are manifested.

The sporangia of the Polypodiaceae, in which family the most familiar and largest number of species are comprised, are united in groups or SORI on the under side of the leaves. They are borne on a cushion-like projection of tissue termed the RECEPTACLE (Fig. 471 *A*), and in many species are covered by a protective membrane, the INDUSIUM, which is an outgrowth of the tissue of the leaf (Fig. 471 *B*, *C*). Each sporangium arises by the division of a single epidermal cell (Fig. 466), and consists, when ripe (Fig. 473), of a capsule attached to the receptacle by a slender multicellular stalk, containing a large number of spores, which only in a few genera (*Asplenium*, *Aspidium*, *Acrostichum*, etc.) are surrounded by a perispore. The wall of the capsule is formed of a single layer of cells. A row of cells with strongly thickened radial and inner walls, extending from the stalk over the dorsal side and top to the middle of the ventral side of the capsule, are specially developed as a ring or ANNULUS, by means of which the dehiscence of the sporangium is effected. This type of annulus is characteristic of the Polypodiaceae.

On drying of the wall of the sporangium the cohesion of the remaining water in the cells of the annulus draws in the thin outer walls of these cells; this causes the annulus to shorten and determines the dehiscence of the sporangium by a tranverse slit between the broad terminal cells of the annulus. When the pull exerted by the cohesive power of the water suddenly gives way, the annulus returns by its own elasticity to its original position, thus effecting the dispersal of the spores. The sporangium remains open owing to the drying and contraction of the thin cell walls ([118]).

The form and insertion of the sori, the shape of the indusium when present, or its absence, all constitute important criteria for distinguishing the different genera. The sori of *Scolopendrium* (Fig. 472) are linear, and covered with a lip-shaped indusium consisting of one cell-layer. They are so disposed in pairs on different sides of every two successive nerves, that they appear to have a double indusium opening in the middle. In the genus *Dryopteris* (*Aspidium*), on the other hand, each sorus is orbicular in form and covered by a peltate or

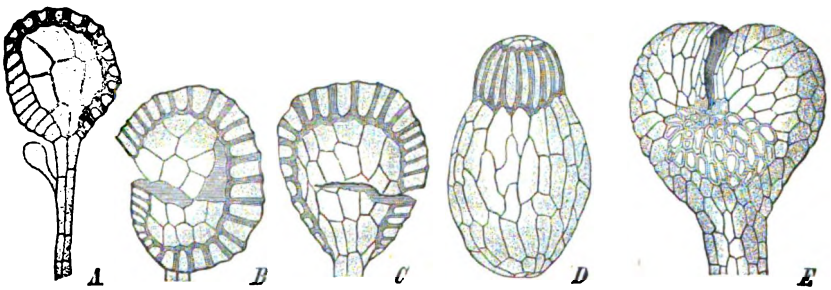


FIG. 473.—Sporangia. *A*, *Dryopteris* (*Aspidium*) *filix mas*; there is a glandular hair at the base. *B* and *C*, *Alsophila armata*, seen from the two sides. *D*, *Aneimia caudata*. *E*, *Osmunda regalis*. (*A-D* × 70 orig.; *E* × 40. After LÜRSSEN.)

reniform indusium attached to the apex of the placenta; a glandular hair is frequently present on the stalk of the sporangium (Fig. 471). The sori of *Polypodium vulgare* are also orbicular, but they have no indusia. In the common Bracken, *Pteridium aquilinum*, the sporangia form a continuous line along the entire margin of the leaf, which folds over and covers them.

Besides the Polypodiaceae the Ferns include other families, mainly represented in the tropics, the sporangia of which differ in the construction of the annulus and in the mechanism of their dehiscence. The sporangia of the Cyatheaceae, to which family belong principally the Tree-Ferns, are characterised by a complete annulus extending obliquely over the apex of the capsule (Fig. 473 *B*, *C*). The Hymenophyllaceae, often growing as epiphytes on Tree-Ferns, have also sporangia, with a complete, oblique annulus. The sporangia of the Schizaeaceae and Gleicheniaceae, on the other hand, have a transversely-placed annulus which, in the former (Fig. 473 *D*), is close to the tip and in the latter above the middle of the sporangium, while in the Osmundaceae, of which the Royal Fern, *Osmunda regalis*, is a familiar example, the annulus is represented merely by a group of thick-walled cells just below the apex of the sporangium (Fig. 473 *E*). In the three last-named families the sporangia open by a median split; in the three preceding families the dehiscence is transverse or oblique. There are thus two

main groups of longicidal and brevicidal Leptosporangiatae, the Eusporangiatae coming closer to the former ([119]).

All the members of the Filices are homosporous. The PROTHALLIUM has usually the form of a small, flat, heart-shaped thallus

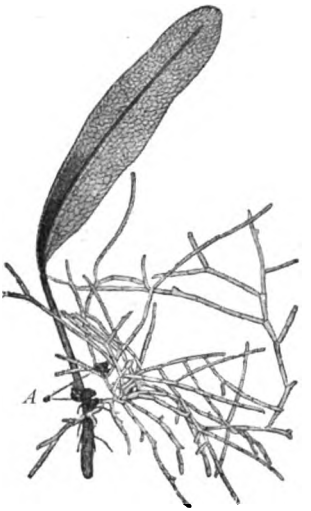


FIG. 474.—*Trichomanes rigidum*. Portion of a prothallus with an archegoniophore (*A*) to which a young plant is attached. (After GOEBEL.)

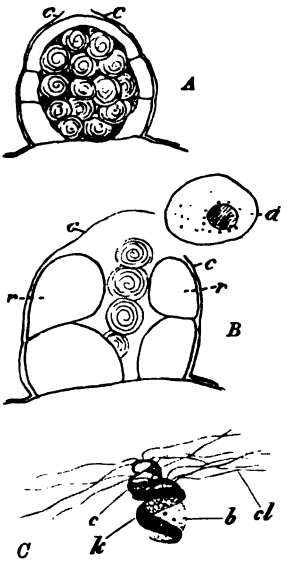


FIG. 475.—*A*, Mature antheridium of *Woodsia ilvensis*; the cuticle (*c*) is ruptured. *B*, Open antheridium; *d*, cap-cell; *r*, swollen annular cells. (After SCHLUMBERGER.) *C*, Spermatozoid of *Struthiopteris germanica*; *k*, nucleus; *cl*, cilia; *b*, vesicle derived from the vacuole; *c*, cytoplasm. (× 850. After SHAW.)

(Fig. 461), bearing the antheridia and archegonia on the under side which is turned from the light.

In certain Hymenophyllaceae (*Trichomanes*) the prothallium is filiform and branched, resembling in structure the protonema of the Mosses, and producing the antheridia and archegonia on special multicellular lateral branches (Fig. 474).

The ANTHERIDIA and ARCHEGONIA ([120]) are similarly constructed in nearly all Leptosporangiatae, and present differences from those of the Eusporangiate Ferns. The antheridia are spherical projecting bodies (Fig. 475), arising on young prothallia by the septation and further division of papilla-like protrusions from single superficial cells. When mature, each antheridium consists of a central cellular cavity, filled

with spermatozoid mother cells, and enclosed by a wall formed of two ring-shaped cells and a lid-cell. The spermatozoid mother cells are produced by the division of the central cell. They are discharged from the antheridium by the pressure exerted by the swollen ring cells, and the consequent rupturing of the lid-cell. Each mother cell thus ejected liberates a spirally coiled spermatozoid. The anterior extremity of the spermatozoid is beset with numerous cilia, while attached to its posterior end is a small vesicle which contains a number of granules, and represents the unused remnant of the contents of the mother cell.

The archegonia arise from the many-layered median portion of older prothallia. They are developed from a single superficial cell, and consist of a ventral portion, embedded in the prothallium, and a neck portion. The neck, which projects above the surface of the

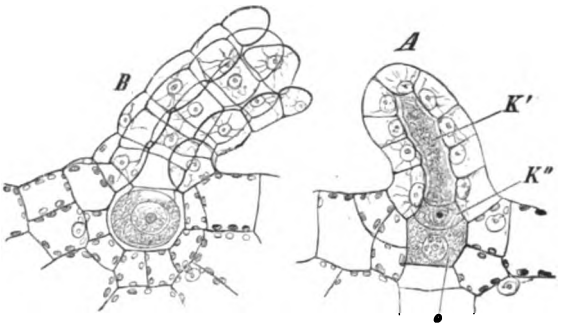


FIG. 476.—*Polypodium vulgare*. *A*, Young archegonium not yet open; *K'*, neck-canal-cell; *K''*, ventral-canal-cell; *o*, egg-cell; *B*, mature archegonium, open. (× 240. After STRASBURGER.

prothallium, consists of a wall composed of a single layer of cells made up of four cell rows (Fig. 476); it encloses the elongated neck-canal-cell. The ventral portion contains the large egg-cell and the ventral-canal-cell immediately above it. As the archegonium matures, the canal-cells become disorganised, and fill the canal with a strongly refractive mucilaginous substance. This swells on the admission of water, and, rupturing the neck at the apex, is discharged from the archegonium, which is now ready for fertilisation. The development of the embryo is represented in Fig. 462.

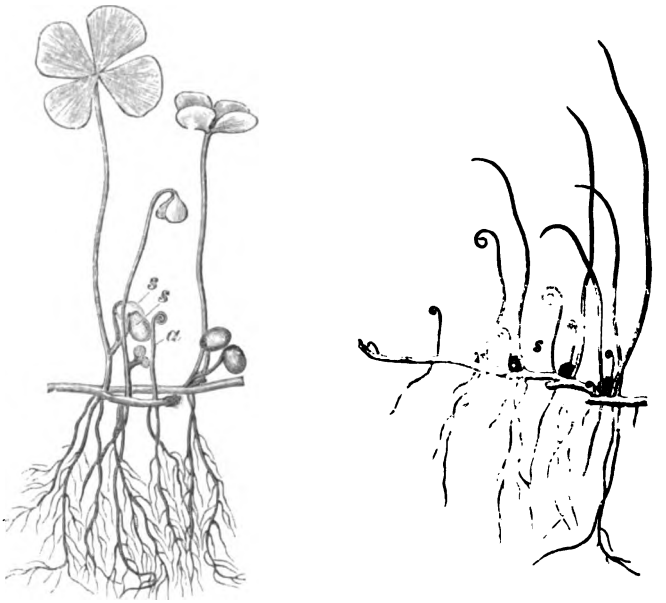
In certain ferns the sporophyte may originate on the prothallus by a process of budding or direct vegetative growth; the sexual organs are not formed or they take no part in the production of the plant (apogamy). Conversely the prothallus may arise directly, without the intervention of spores, from the tissues of the leaf (apospory).

OFFICIAL.—*Dryopteris* (*Aspidium*) *filix mas*, provides FILIX MAS.

The long silky brown hairs from the base of the leaf-stalks of various Tree-Ferns, especially *Cibotium Barometz*, and other species of this genus, in the East Indies and the Pacific Islands, are used as a styptic, and also for stuffing cushions, etc.

Order 2. Hydropterideae (Water-Ferns) (121-123)

The Water-Ferns include only a few genera, which are more or less aquatic in habit, growing either in water or marshy places. They are all heterosporous. The macro- and micro-sporangia do not develop, like those of the Filices, on the under side of the leaves, but are enclosed in special receptacles at their base, constituting sporangial fructifications or sporocarps. The wall of the sporangium, which consists of a single layer of cells, has no annulus. The spores are surrounded by a specially developed perisporium.



A B

FIG. 477.—*A*, *Marsilia quadrifolia*; *a*, young leaf; *s*, sporocarps. *B*, *Pilularia globulifera*; *s*, sporocarp. (After BISCHOFF, reduced.)

The Water-Ferns are divided into two families: *Marsiliaceae*, including three genera, and *Salviniaceae*, with two genera.

To the **Marsiliaceae** belongs the genus *Marsilia*, of which the European *M. quadrifolia* (Fig. 477 *A*) may be taken as an example. This species has a slender, creeping, branched axis, bearing at intervals single leaves. Each leaf has a long erect petiole, surmounted by a compound lamina composed of two pairs of leaflets inserted in close proximity. The stalked oval sporocarps (*s*) are formed in pairs above the base of the leaf-stalk, or in other species they are more numerous. Each of them corresponds in development to the quadripinnate sterile lamina, but is not divided into pinnae. The young leaves, as in the Filices, are circinate.

Pilularia also grows in bogs and marshes. *P. globulifera* is found in Britain. It differs from *Marsilia* in its simple linear leaves, at the base of which occur the spherical sporocarps, which arise singly from the base of each sterile leaf-segment; the sporocarp corresponds to a segment of the leaf (Fig. 477 *B*).

The **Salviniaceae** contains only free-floating aquatic plants belonging to the two genera *Salvinia* and *Azolla*. In *Salvinia natans*, as representative of the first genus, the sparingly-branched stem gives rise to three leaves at each node. The two upper leaves of each whorl are oval in shape, and developed as floating foliage leaves; the third, on the other hand, is submerged, and consists of a number of pendent, filamentous segments which are densely covered with hairs, and assume the functions of the missing roots. The sporocarps have an entirely different mode of development from those of the Marsiliaceae; they are spherical, and are borne in small groups on the submerged leaves at the base of the filamentous segments (Fig. 478 *A*). The sporangia are produced within the sporocarp from a column-like receptacle, which corresponds in origin to a modified leaf-segment. The envelope of the sporocarp is equivalent to an indusium; it arises as a new growth in the form of an annular wall, which is at first cup-shaped, but ultimately closes over the receptacle and its sorus of sporangia.

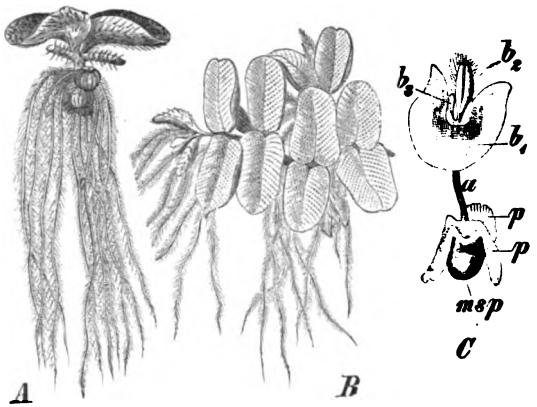


FIG. 478.—*Salvinia natans*. *A*, Seen from the side; *B*, from above (after BISCHOFF, reduced). *C*, An embryonic plant; *msp*, macrospore; *p*, prothallium; *a*, stem; b_1, b_2, b_3, the first three leaves; b_1, the so-called scutiform leaf. (× 15. After PRINGSHEIM.)

The second genus, *Azolla*, is chiefly tropical, represented by small floating plants, profusely branched, and beset with two-ranked closely crowded leaves. Each leaf consists of two lobes, of which the upper floats on the surface of the water, while the lower is submerged, and assists in the absorption of water. A small cavity enclosed within the upper lobe, with a narrow orifice opening outwards, is always inhabited by filaments of the Blue Green Alga, *Anabaena azollae*. From the fact that hairs grow out of the walls of the cavity between the algal filaments, the existence of a symbiotic relation between the two plants would seem to be indicated. *Azolla*, unlike *Salvinia*, possesses long slender roots developed from the under side of the stem. The sporocarps are nearly spherical, and produced usually in pairs on the under side of the leaves of some of the lateral branches.

In the structure of the sporangia and spores, and in the development of the prothallia, the Hydropterideae differ in some respects from the Filices. These differences may be best understood on reference to *Salvinia natans* ([121]) as an example. The sporocarps contain either numerous microsporangia or a smaller number of macrosporangia (Fig. 479 *A*, *ma*, *mi*). In structure both forms of sporangia resemble the sporangia of the Leptosporangiate Ferns; they are stalked, and have,

when mature, a thin wall of one cell-layer, but no annulus (*B*, *D*). The MICROSPORANGIA enclose a large number of microspores, which, as a result of their development in tetrads from the mother-cells, are disposed in groups of four (*C*), and embedded in a hardened frothy mass filling the cavity of the sporangium. This frothy interstitial substance is derived from the tapetal cells, which gradually lose their individuality and wander in between the spore-mother-cells.

The microspores germinate within the microsporangium, which does not open; each germinating microspore puts out a short tubular male prothallium, which pierces the sporangial wall. Two antheridia are developed in this by successive divisions (Fig. 480). Each antheridium produces four spermatozoids, which are set free by the rupture of the cell walls. Although the whole male prothallium is thus greatly reduced, it nevertheless exhibits in its structure a resemblance to the prothallia of the Filices.

The MACROSPORANGIA are larger than the microsporangia, but their walls

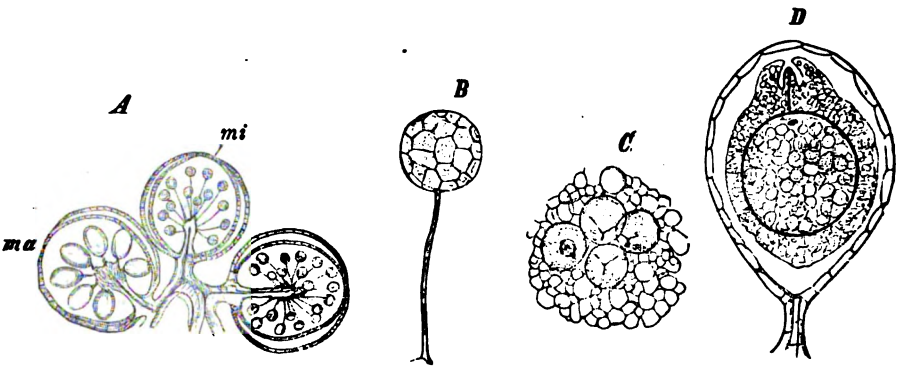


FIG. 479.—*Salvinia natans*. *A*, Three sporocarps in median longitudinal section; *ma*, macrosporocarp; *mi*, microsporocarp (× 8); *B*, a microsporangium (× 55); *C*, portion of the contents of a microsporangium, showing four microspores embedded in the frothy interstitial substance (× 250); *D*, a macrosporangium and macrospore in median longitudinal section (× 55). (After STRASBURGER.)

consist similarly of one cell-layer (Fig. 479 *D*). Each macrosporangium produces only a single large macrospore, which develops at the expense of the 32 spores originally formed. The macrospore is densely filled with large angular proteid grains, oil globules, and starch grains; at its apex the protoplasm is denser and contains the nucleus; the membrane of the spore is covered by a dense brown exospore, which in turn is enclosed in a thick frothy envelope, the perispore, investing the whole spore and corresponding to the interstitial substance of the microspores, and like this formed from the dissolution of the tapetal cells. The macrospore remains within the sporangium, which is eventually set free from the mother plant and floats on the surface of the water. On the germination of the macrospore, a small-celled female prothallium is formed by the division of the denser protoplasm at the apex, while the large underlying cell does not take part in the division, but from its reserve material provides the developing prothallium with nourishment. The spore wall splits into three valves, the sporangial wall is ruptured, and the green prothallium protrudes as a small saddle-shaped body. On it three to five archegonia are produced, but only the fertilised egg-cell of one of them develops into an embryo, the foot of which remains for a time sunk in

the venter of the archegonium (Fig. 481). The first leaf of the germ plant is shield-shaped (Fig. 478 *C*) and floats on the surface of the water.

The development of *Azolla* ([121a]) proceeds in a similar manner, but the sporangia and spores exhibit a number of distinctive peculiarities. The micro- and macrosporocarps at first develop alike; in each a single macrosporangium is laid down surrounded by the tubular indusium, and from the stalk of the macrosporangium the microsporangia grow out. In the microsporocarp only the microsporangia develop; in the macrosporocarp, on the other hand, only the macrosporangium becomes mature.

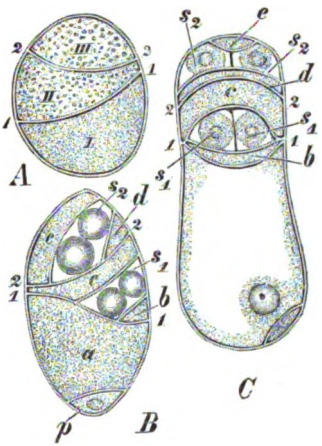


FIG. 480.—*Salvinia natans.* Development of the male prothallium. *A*, Division of the microspore into three cells *I-III* (× 860); *B*, lateral view; *C*, ventral view of mature prothallium (× 640). Cell *I* has divided into the prothallium cells *a* and *p*; the latter is the rhizoid cell; cell *II* into the sterile cells *b*, *c*, and the two cells s_1, each of which has formed two spermatozoid mother-cells; cell *III* into the sterile cells *d*, *e*, and the two cells s_2. The cells s_1s_1 and s_2s_2 represent two antheridia; the cells *b*, *c*, *d*, *e*, their wall cells. (After BELAJEFF.)

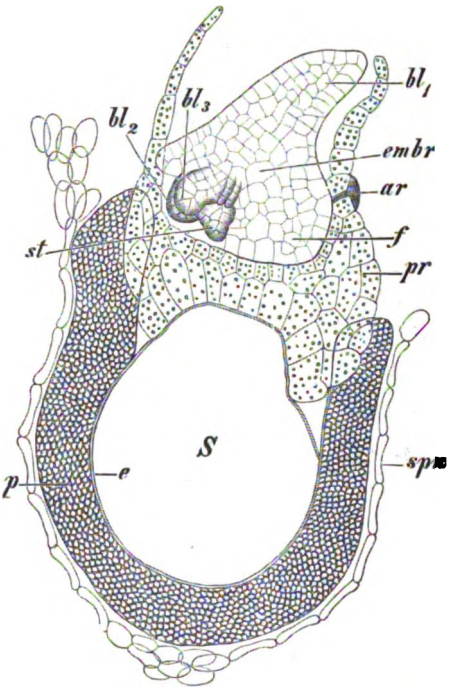


FIG. 481.—*Salvinia natans.* Embryo in longitudinal section; *pr*, prothallium; *S*, spore-cell; *e*, exinium; *p*, perispore; *spw*, sporangial wall; *ar*, archegonium; *embr*, embryo; *f*, foot; bl_1, bl_2, bl_3, the first three leaves; *st*, apex of stem. (× 100. After PRINGSHEIM.)

The 64 spores of the microsporangia are aggregated into several nearly spherical balls or massulae, formed from the interstitial substance derived from the protoplasm of the tapetal cells. Each massula, enclosing a number of spores, is beset externally with barbed, hook-like outgrowths of the interstitial substance (glochidia). On the rupture of the sporangia the massulae are set free in the water, and are carried to the macrospores, to which they become attached. In the macrosporangium 32 macrospores are laid down, but only one comes to maturity; in the course of its development it supplants all the other sporogenous cells, and finally the sporangial wall itself becomes flattened against the inner wall of the sporocarp, frequently undergoing at the same time partial dissolution. The macrospore is enveloped by a spongy perispore, whose outer surface exhibits

numerous depressions and protuberances prolonged into filaments. At the apex of the spore the perispore expands into three pear-shaped appendages. The massulae become attached to the perispore. The wall of the sporocarp is ruptured at its lower portion, the apical portion remaining attached to the spore in the form of an ampulla-like covering. The formation of the prothallia is effected in essentially the same way as in *Salvinia*, except that only one

FIG. 482. — *Marsilia salvatrix*. *A*, Sporocarp (nat. size); *st*, stalk. *B*, Sporocarp opening in water, showing the emerging mucilaginous cord. *C*, The mucilaginous cord (*g*) ruptured and fully extended; *sr*, soral chambers; *sch*, hard shell of the sporocarp. *D*, An immature sorus; *ma*, macrosporangia; *mi*, microsporangia. (After J. SACHS and J. HANSTEIN.)

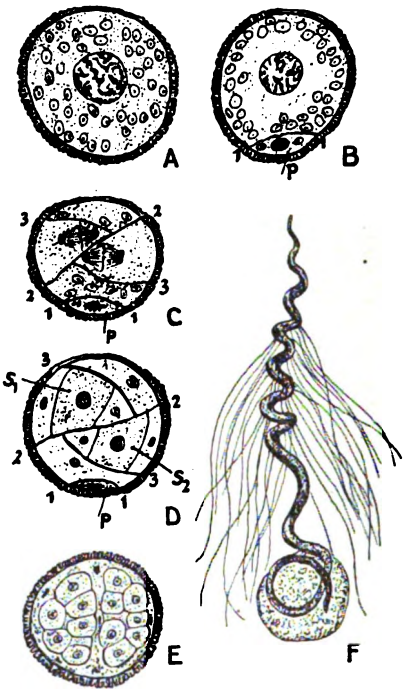


FIG. 483.— *Marsilia quadrifolia*. Development of the male prothallus from the spore. *A*, The spore; *B*, a small prothallial cell (*p*) is cut off by the wall (*1*); *C* and *D*, further divisions, s_1, s_2, the mother-cells of the spermatogenous tissue in the two antheridia; *E*, mature condition, two groups of 16 spermatozoids having developed from s_1 and s_2, lie in the substance derived from the breaking down of the peripheral sterile cells; *F*, a spermatozoid, highly magnified, showing the cilia arising from the elongated blepharoplast lying beside the spirally-wound nucleus. (After LESTER W. SHARP.)

antheridium with eight spermatozoids arises on each of the small male prothallia protruding from a massula.

The sporocarps of the Marsiliaceae ([122]) have a more complicated structure: those of *Pilularia globulifera* are divided into four chambers, each with a single sorus; in *Marsilia* they enclose numerous sori (14-18) disposed in two rows. The sori in both genera contain both micro- and macro-sporangia. These arise as in many ferns from superficial marginal cells and come to lie in cavities by the upgrowth of the surrounding tissue. The outer layers of this become differentiated to form a hard coat.

After a period of rest the sporocarps germinate in water. In *Pilularia* the tissue surrounding the sori swells, bursts the hard coat, and emerges as a mucilaginous mass; this contains the sporangia from which, by further swelling of the walls, the spores become free. The development of the prothalli and fertilisation take place in the mucilaginous mass that persists for some days. The sporocarp of *Marsilia*, on the other hand, opens as two valves. A cartilaginous cord of tissue lying within the ventral suture of the sporocarp swells greatly, and splitting the ventral suture emerges bearing with it the sori, enclosed by membranous investments (Fig. 482).

From the microspore a reduced male prothallus is developed within the spore-membrane. This when mature contains two antheridia, each with 16 spermatozoids, and liberates these as cork-screw-like, spirally-wound, motile spermatozoids bearing numerous cilia (Fig. 483).

The thick-walled macrospore has, as in the case of *Salvinia*, denser protoplasm at the summit. This is cut off from the large cell enclosed in the spore-coat by a wall, and develops into a small green saddle-shaped prothallus composed of a few cells. This only forms a single archegonium and is thus greatly reduced (Fig. 484).

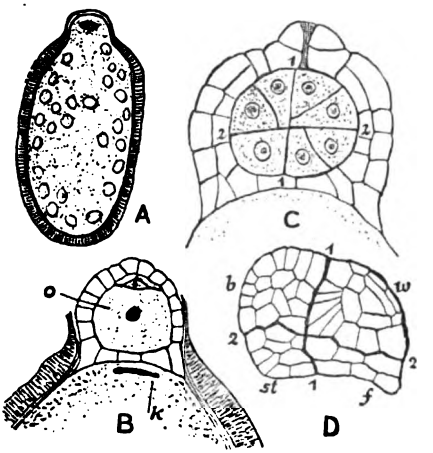


FIG. 484.—*Marsilia vestita*. *A*, Macrospore with the nucleus at the summit in the protoplasm from which the female prothallus shown in *B* is derived; *o*, egg-cell of the archegonium, with the ventral-canal-cell and neck-canal-cell above it; *k*, nucleus of the large cell enclosed in the spore-membrane. *C*, Young embryo in the archegonium showing the first divisions; *1*, basal wall; *2*, quadrant walls. *D*, Later stage; *w*, young root; *b*, first leaf; *st*, stem; *f*, foot. (*A* × 60; *B* × 360; *C* × 525; *D* × 260. After D. CAMPBELL.)

The embryogeny follows the type of the Leptosporangiate Ferns, the egg-cell dividing first by a longitudinally-placed basal wall and then by transverse walls into quadrants; these then divide to give the octants. The first leaf and the root arise from the two upper pairs of octants; the lower pairs give rise to the foot and the stem-apex (Fig. 484 *C*, *D*).

The prothallus grows for a time enclosing the embryo, and forms a few rhizoids from its lower cells. If fertilisation does not take place, a somewhat longer-lived prothallus results, which does not, however, form further archegonia.

An apogamous formation of the embryo has been shown to exist in certain Australian species of *Marsilia* belonging to the group of *M. Drummondii* ([123]).

CLASS II

Equisetinae (Horse-tails) ([1, 92, 112, 115, 124])

Order 1. Equisetaceae

The Equisetaceae include only the one genus *Equisetum*, comprising 20 species, found widely distributed over the whole world. The genus can be

traced back to the Triassic period. Developed partly as land, partly as swamp plants, they may always be distinguished by the characteristic structure and habit of the asexual generation. They have a branching, underground rhizome on which arise erect, aerial haulms, usually of annual growth. The rhizome of the common Horse-tail, *Equisetum arvense*, develops also short tuber-like branches which serve as reservoirs of reserve material and hibernating organs (Fig. 486). The aerial haulms remain either simple, or they give rise to branch whorls, and these in turn to whorls of a higher order. All the axes are formed of elongated internodes; they have a central pith-cavity and a peripheral series of smaller air channels. The collateral vascular bundles form a single circle, as seen in transverse section (Fig. 485).

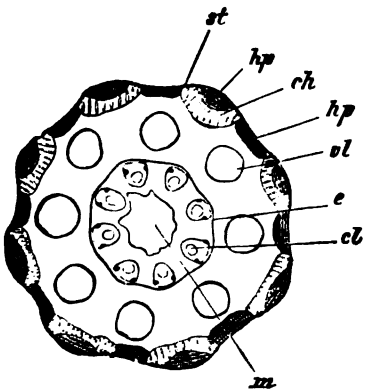


FIG. 485.—*Equisetum arvense*. Transverse section through the stem. *m*, Lysigenic medullary cavity; *e*, endodermis; *cl*, carinal canals in the collateral bundles; *vl*, vallecular cavities; *hp*, sclerenchymatous strands in the furrows and ridges; *ch*, tissue of the primary cortex containing chlorophyll; *st*, rows of stomata. (× 11. After STRASBURGER.)

At each node is borne a whorl of scale-leaves pointed at the tips, and united below into a sheath closely enveloping the base of the internode. The lateral branches are developed in the axils of the scale-leaves, but not having space to grow upwards they pierce the narrow sheath. As a result of the reduction of the leaf laminae, the haulms themselves assume the function of assimilation, and for that purpose their cortical tissue under the epidermis is provided with chlorophyll.

The SPORANGIA are borne on specially-shaped leaves or sporophylls. The sporophylls are developed in whorls, but are closely aggregated at the tips of the erect fertile shoots into a cone (Fig. 486), which is sometimes spoken of as a flower, from the correspondence in its structure to the male flower of the Conifers. The lowest whorl is sterile, and forms a collar-like protuberance. The sporophylls (Fig. 486 *B*, *C*) are stalked and have a peltate expansion, on the under side of which are borne the (5-10) sac-like sporangia. In the young sporangium the sporogenous tissue is surrounded by a wall consisting of several cell layers, but eventually the tapetal cells of the inner layer become disorganised, and their protoplasm penetrates between the developing spores, forming the periplasmodium. At maturity the wall of the sporangium consists only of the outermost of the original layers; the cells of this are provided with annular and spiral thickenings. The sporangia thus resemble the homologous pollen-sacs of Phanerogams. The dehiscence is determined by the cohesive force of the diminishing amount of water in the cells of the outer layer and the contraction of the thin parts of the cell walls on drying. The sporangia split longitudinally, and set free a large number of green spores, which are nearly spherical in shape, and have peculiarly constructed walls. In addition to the endospore and exospore, the spores are overlaid with a perispore deposited by the periplasmodium, and consisting of two spiral bands (elaters) which are attached to the spores only at their point of intersection (Fig. 486 *D*). On drying, the spiral bands loosen and become uncoiled; when moistened they close again

around the spore. By means of their hygroscopic movements they serve to hook

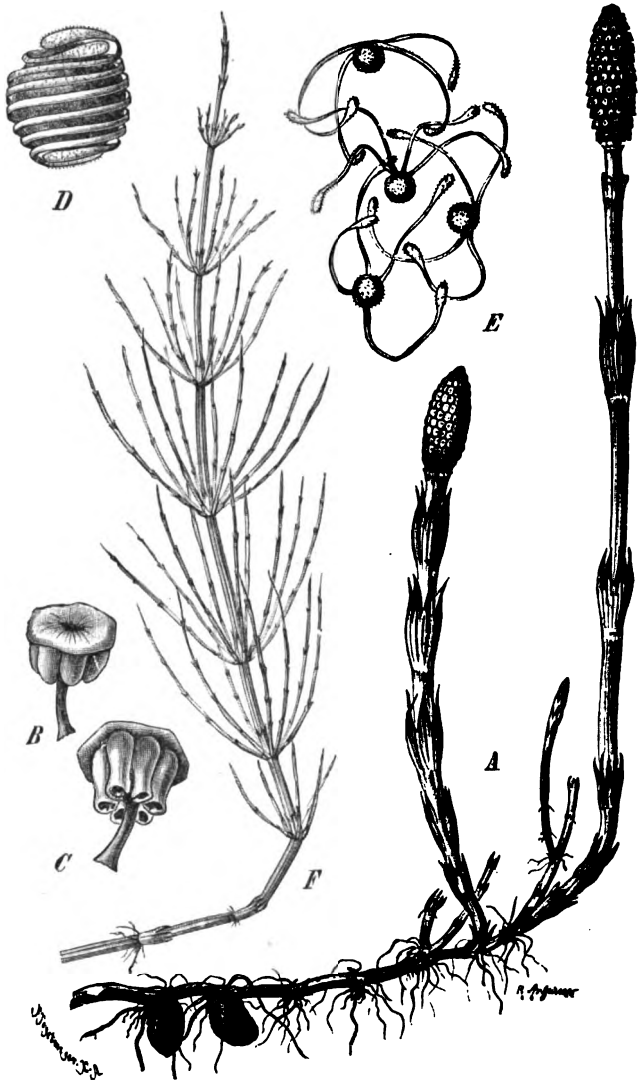


FIG. 486.—*Equisetum arvense*. *A*, Fertile shoots, springing from the rhizome, which also bears tubers; the vegetative shoots have not yet unfolded. *F*, Sterile vegetative shoot. *B*, *C*, Sporophylls bearing sporangia, which in *C* have opened. *D*, Spore showing the two spiral bands (elaters) of the perispore. *E*, Dry spores showing the expanded spiral bands. (*A*, *F*, ½ nat. size. *B*, *C*, *D*, *E*, enlarged.)

together the spores, and in this way assure the close proximity of the unisexual prothallia which the latter produce (Fig. 486 *E*).

In certain species some of the aerial haulms always remain sterile, branching profusely, while others which produce the terminal cones either do not branch at all, or only at a later stage, and then sparingly. This distinction between the sterile and fertile haulms is most marked in *Equisetum arvense* and *Equisetum Telmateja*, in both of which the fertile shoots are entirely unbranched and terminate in a single cone (Fig. 486). Resembling in their mode of life a parasite upon the rhizome, they are otherwise distinguished from the vegetative haulms by their lack of chlorophyll and their light yellow colour.

Equisetum giganteum, growing in South America, is the tallest species of the

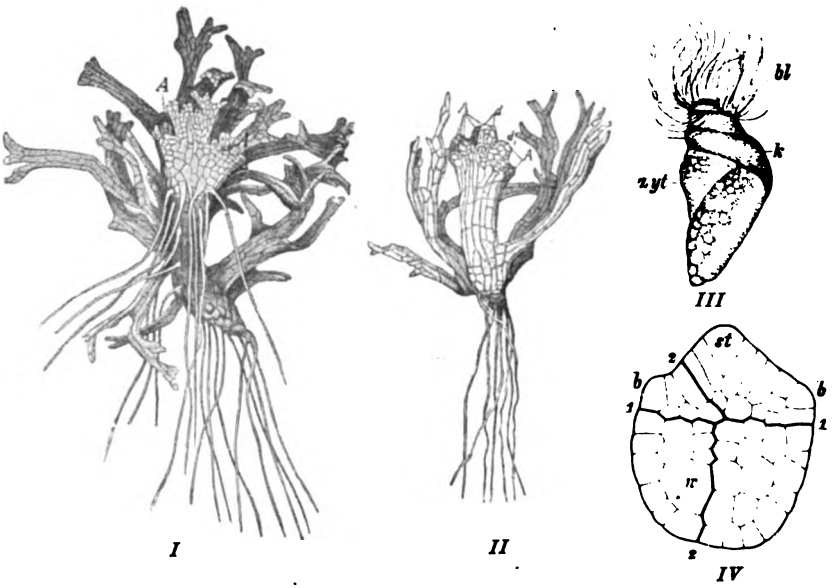


FIG. 487.—*Equisetum pratense*. *I*, Female prothallium from the under surface, showing the archegonia (*A*). *II*, Male prothallium with antheridia (*A*); *d*, cover cells of antheridia. (*I* × 17, *II* × 12. After GOEBEL.) *III*, *Equisetum arvense*. Spermatozoid: *k*, nucleus; *bl*, cilia-forming blepharoplast with cilia; *zyt*, cytoplasm. (× circa 1250. After SHARP.) *IV*, *Equisetum arvense*. Embryo: *1*, *2*, octant walls. The stem (*st*) and first leaf-whorl (*b*) arise from the upper half, and the root (*w*) and foot from the lower half. (× 165. After SADEBECK.)

genus; its branched haulms, supported by neighbouring plants, attain a height of over twelve metres, and are about two cm. in diameter.

The spores are all of one kind, and on germination give rise to thalloid PROTHALLIA which are generally dioecious (Fig. 487). The female prothallia are larger than the male, and, branching profusely, are prolonged into erect ruffled lobes at whose base the archegonia are produced. In structure the archegonia resemble those of the Ferns, but the upper cells of the four longitudinal rows of cells constituting the neck are more elongated and, on opening, curve strongly outwards. The spermatozoids, like those of ferns, bear numerous cilia. The first leaves of the embryo are arranged in a whorl and encircle the apex of the stem. The growth of the embryo is effected by the division of a three-sided apical cell (Figs. 487 *IV*, 100, 101).

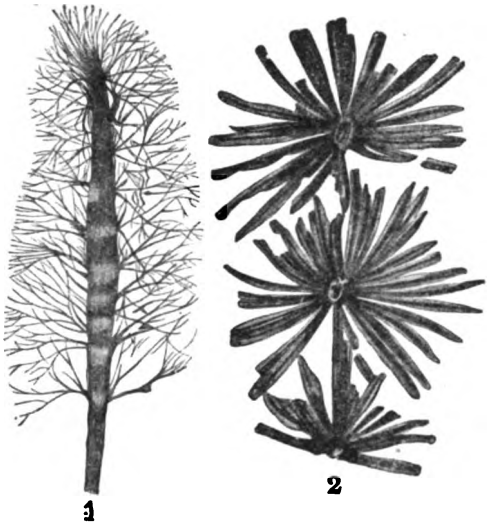


FIG. 488.—*1*, *Archaeocalamites radiatus*. (After STUR.) *2*, *Annularia stellata*. (After SEWARD.) From LOTSY, *Botan. Stammesgeschichte*.

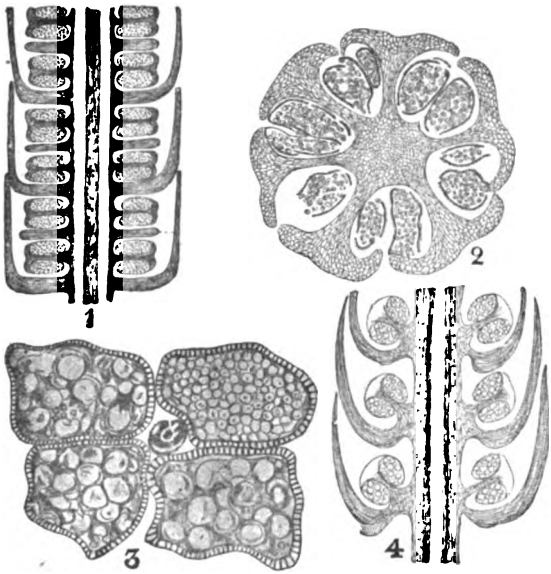


FIG. 489.—*1*, *Calamostachys Binneyana*, Cone in longitudinal section. *2*, The same in transverse section. *3*, *Calamostachys Casheana*, Transverse section of a sporangiophore, showing the stalk and three macrosporangia and one microsporangium. *4*, *Palaeostachya*, Longitudinal section of cone with axillary sporangiophores. (After SCOTT and HICKLING. From LOTSY.)

The outer epidermal walls of the stem are more or less strongly impregnated with silica. In *Equisetum hiemale*, and to a less degree in *Equisetum arvense*, the silicification of the external walls is carried to such an extent that they are used for scouring metal utensils and for polishing wood.

Poisonous substances are formed in some species of *Equisetum*, and hay with which the shoots are mixed is injurious to cattle.

Order 2. Calamariaceae [132]

This extinct order was highly developed in the palaeozoic period, especially in the Carboniferous, when it was represented by numerous species. The plants resembled the Horse-tails in general habit, but in some cases attained the size of trees 30 metres high; the hollow stem, which bore whorls of branches at the nodes, was covered with a periderm, and underwent secondary thickening. The leaves (*Annularia*, Fig. 488) stood in alternating whorls; their form was narrowly lanceolate and at their bases they united into a sheath. In the most ancient type, *Archaeocalamites* (Fig. 488), they were dichotomously divided, and thus more fern-like. The cones or flowers had in this genus the same structure as those of *Equisetum*; in most cases they were more complicated, whorls of superposed scale-leaves separating the whorls of specialised sporangiophores. Each of the latter was a stalked peltate disc bearing, on its under side, four sporangia (Fig. 489). In *Calamostachys* the sporangiophores are placed some distance above the corresponding sporophylls, while in *Palaeostachya* they stand in the axils of the latter. They may be regarded morphologically as special outgrowths of the scale-like sporophylls. It is an interesting fact that heterosporous as well as homosporous forms occur among the Calamarieae.

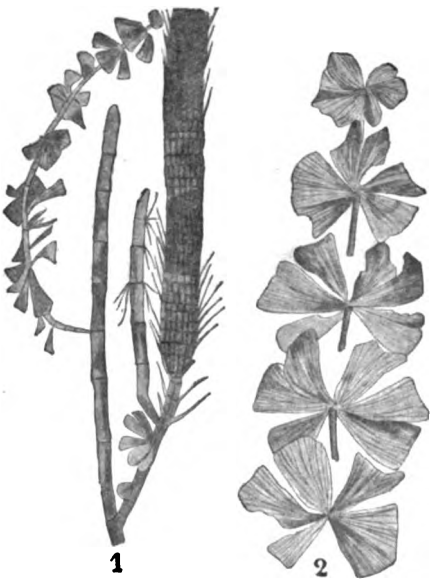


FIG. 490.—*1*, *Sphenophyllum*, showing the branched stem with both linear and wedge-shaped leaves and, on the right, an elongated cone. (After SCOTT.) *2*, *S. emarginatum*. (After SEWARD.) From LOTSY.

CLASS III

Sphenophyllinae [132]

This small class occupies an intermediate position between the Equisetineae and the Lycopodinae.

The Sphenophyllinae were represented by two genera in palaeozoic times. *Cheirostrobus* from the Lower Carboniferous had complex cones of similar structure to those of the Calamarieae, but approached *Lepidodendron* in anatomical structure. The species of *Sphenophyllum* which lived from the Devonian to the Permian periods were herbaceous land-plants with elongated internodes. The stems, which underwent

secondary growth in thickness, bore superposed whorls of, usually six, wedge-shaped or dichotomously-divided leaves. The spike-like cones resembled somewhat those of *Equisetum*; each sporophyll bore one to four homosporous sporangia (Fig. 490).

CLASS IV

Lycopodinae (Club Mosses) ([1, 92, 112, 115])

The Lycopodinae are sharply distinguished from the other Pteridophyta, by their general habit and the mode of their sporangial development.

They were abundantly represented in the palaeozoic period and included arborescent forms belonging mainly to the extinct orders of Sigillariaceae and Lepidodendraceae.

The numerous existing species are all herbaceous plants. The most important genera, representing as many orders, are *Lycopodium*, *Selaginella*, and *Isoetes*.

The dichotomous branching of the stem (Figs. 139, 141) and root and the simple form of the leaves are characteristic of the sporophyte. The two first-named genera have elongated stems and small leaves; *Isoetes*, on the other hand, has a tuberous stem and long awl-shaped leaves. Unlike the fertile leaves of the Filicinae and Equisetinae, which always bear numerous sporangia, the sporophylls of the Lycopodinae produce the sporangia singly, at the base of the leaves or in their axils. Although in many cases scarcely distinguishable from the sterile leaves, the sporophylls are frequently distinctively shaped, and, like those of *Equisetum*, aggregated at the ends of the fertile shoots into terminal spike-like cones or flowers. Compared with the leaves, the sporangia are relatively large and have a firm wall of a number of layers of cells. The innermost layer of the sporangial wall, the tapetal layer, is not absorbed. On this account no perispore is deposited on the spore-wall. The developing spores are surrounded with a mucilaginous nutritive fluid. The sporangia have no annulus. Except in the case of *Isoetes*, the spores of which become free by the decay of the sporangial wall, the sporangia dehisce by longitudinal slits, which divide the wall into two valves; the slits occur where rows of cells of the wall have remained thin. *Lycopodium* is homosporous, while *Selaginella* and *Isoetes* are heterosporous. The heterosporous forms produce only greatly modified and reduced prothallia; in the genus *Lycopodium*, on the other hand, the prothallia are well developed, and show certain resemblances to those of the Ophioglossaceae. The simplified prothalli of *Selaginella* and *Isoetes* may be compared to early stages of the prothalli of *Lycopodium* which have proceeded to form gametes early without undergoing vegetative development.

The Lycopodiaceae and the Selaginellaceae agree in the segmentation of the embryo, which in both is characterised by possessing a suspensor, and in the

structure of the spermatozoids, which are biciliate. The Isoetaceae, on the other hand, have multiciliate spermatozoids and the embryo has no suspensor. On these grounds the two sub-classes of *Lycopodinae biciliatae* and *Lycopodinae pluriciliatae* may be distinguished. Herbaceous Lycopods which are the forerunners of *Lycopodium* and *Selaginella* are known in the Carboniferous, while *Isoetes* is only known with certainty from the Lower Cretaceous.

Order 1. Lycopodiaceae (185)

The numerous widely-distributed species of the genus *Lycopodium* (Club Moss) are for the most part terrestrial plants; in the tropics many pendulous

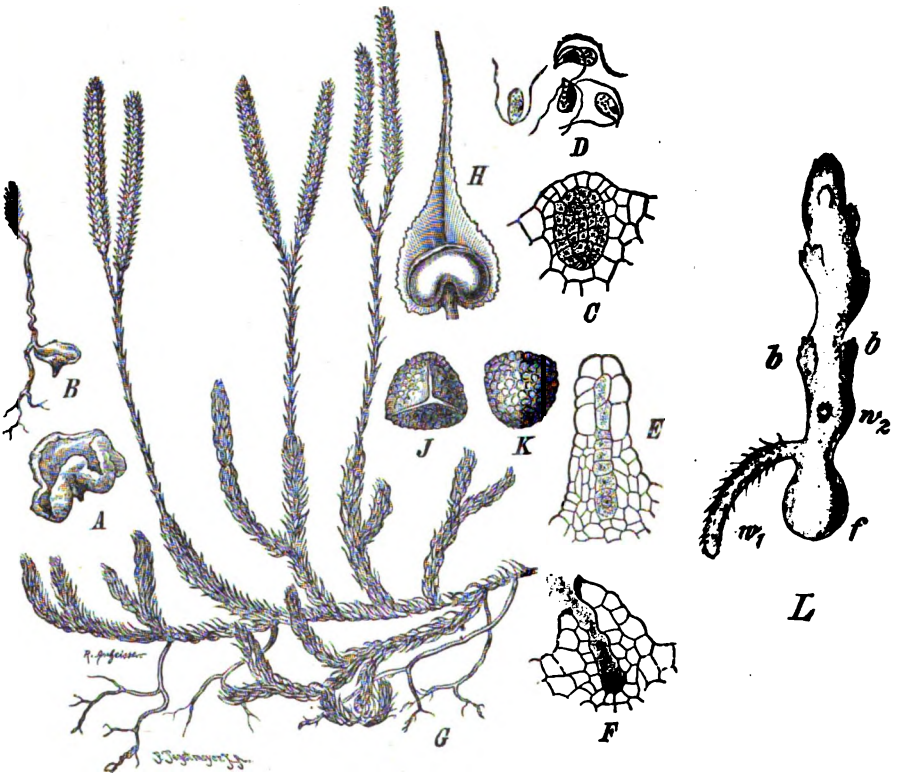


FIG. 491.—*Lycopodium clavatum*. *A*, Old prothallus. *B*, Prothallus with young plant attached. *C*, Antheridium in vertical section. *D*, Spermatozoids. *E*, Young archegonium, the neck still closed. *F*, Open archegonium ready for fertilisation. *G*, Plant bearing cones (½ nat. size). *H*, Sporophyll with an opened sporangium. *J*, *K*, Spores from two points of view. *L*, A young subterranean sporeling still without chlorophyll (× 10); *f*, foot; *w*, root; *b*, scale-leaves. (*A-F* and *L* after BRUCHMANN.)

epiphytic forms also occur. In *Lycopodium clavatum*, one of the commonest species, the stem, which is thickly covered with small, awl-shaped leaves, creeps along the ground; it branches dichotomously, and gives rise to ascending

lateral branches, while from the under side spring the dichotomously-branched roots (Fig. 491). The cone-like flowers, consisting of the closely-aggregated sporophylls, are situated in groups of two or more at the ends of the forked erect shoots. The sporophylls are not like the sterile leaves in shape; they are broader and more prolonged at the tip; each bears a large reniform sporangium on the upper side at the base. The sporangium opens into two

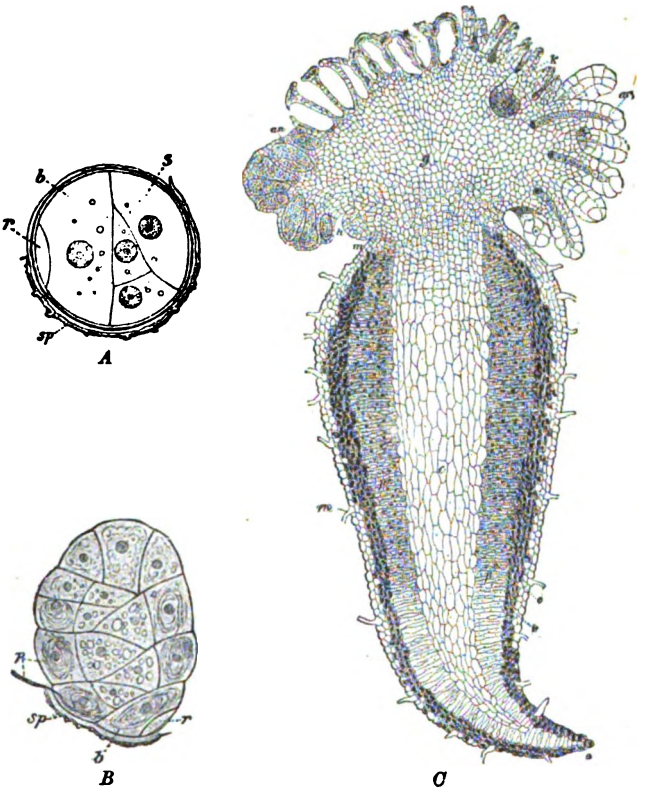


FIG. 492.—*A*, Germinating spore of *Lycopodium annotinum*; *r*, rhizoid cell; *b*, basal cell; *s*, apical cell; *sp*, spore-membrane (× 580). *B*, Older stage of the prothallus of the same species, showing the endophytic fungus (*p*) in the lower cells, and the apical cell divided into three meristematic cells (× 470). *C*, *Lycopodium complanatum*. Prothallus with antheridia (*an*), archegonia (*ar*), and a young embryo (*k*) (× 26). (After BRUCHMANN.)

valves and sets free numerous minute spores (Fig. 491 *H*). *Lycopodium Selago* differs in habit from the other species; its bifurcately-branched stems are all erect, and the fertile are not distinct from the vegetative regions of the shoots.

The spores of the Lycopodiums are all of one kind, and in consequence of their formation in tetrads are of a tetrahedral though somewhat rounded shape. The exospore is covered with a reticulate thickening (Fig. 491 *J*, *K*).

The prothallia developed from the spores show a remarkable variety in the

group. The prothallia of *Lycopodium clavatum* (Fig. 491 *A*, *B*) and the closely related *L. annotinum* are small, white, tuberous structures, which live as subterranean saprophytes. At first top-shaped, they become converted by the continued marginal growth into cup-shaped lobed bodies, which may attain a size of two centimetres. Long rhizoids spring from the lower surface, while the upper surface bears numerous antheridia and archegonia. The spores only germinate after six to seven years, forming at the expense of their reserve materials a prothallus of five cells. Further development only takes place when fungal hyphae enter the lowest cells (Fig. 492 *A*, *B*). The endophytic fungus is confined to the peripheral tissues of older prothalli; it may emerge through the specialised basal cells of the rhizoids and invest the latter ([125a]). Only after twelve to fifteen years is the prothallus sexually mature, so that its life may last some twenty years. In *L. complanatum* (Fig. 492 *C*) the subterranean prothalli are turnip-shaped, in *L. Selago* rounded or elongated cylindrical and dorsiventral. The prothalli of the latter may be developed on the surface of the soil, in which case they are green. In the case of *L. inundatum*, the prothalli of which are found on damp peaty soil, and in the tropical *L. cernuum*, with erect profusely-branched shoots, the prothalli are poor in chlorophyll and are attached to the soil by rhizoids; they have the form of small, half-buried, cushion-like masses of tissue, which give rise to green, aerial, thalloid lobes. The archegonia occur at the base of these lobes, the antheridia also on their surface. All Lycopod prothalli have fungal filaments forming a mycorrhiza in their peripheral tissue.

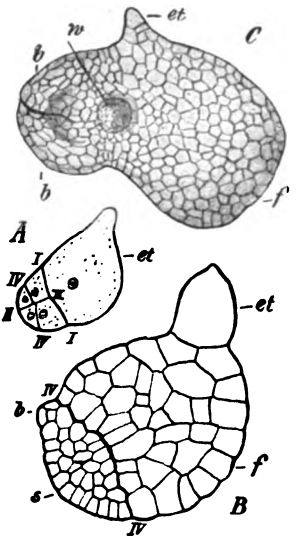


FIG. 493.—Development of the embryo in *Lycopodium complanatum*. *A*, Embryo showing the first divisions; the basal wall *I* separates the suspensor (*et*) from the body of the embryo; the transversal walls *II* and *III* (the latter being in the plane of the section) together with the transverse wall *IV* give rise to two tiers of four cells; the tier next the suspensor gives rise to the foot, the terminal tier forms the shoot (× 112). *B*, Embryo of medium age; *s*, apex of stem; *b*, rudiment of leaf; *f*, foot (× 112). *C*, Embryo shortly before breaking out of the prothallus; *bb*, the two first leaves covering the apex of the stem; *w*, the first root (× 40). (After BRUCHMANN.)

The prothallia are all monoecious. The antheridia are somewhat sunk in the tissue (Fig. 491 *C*) and enclose numerous spermatozoid mother-cells, in which small oval spermatozoids, with two cilia attached below the apex, are formed. The archegonia (Fig. 491 *E*, *F*) are constructed like those of the Ferns, but the upper cells of the neck become disorganised on opening. The number of neck-canal-cells differs in the various species (1, 3-5, or 6-10).

The embryo (Fig. 493) remains during its development enclosed in the prothallus. It has a spherical, in *L. complanatum* club-shaped and irregular, foot which serves as an absorbent organ for the sporeling. Beneath the foot the young shoot forms; the first leaves are scale-like, and from the basal portion of the shoot the first root develops. The suspensor is situated between the shoot and the foot; it serves as the first absorbent and nourishing organ of the embryo.

The spores of *Lycopodium clavatum* and other species are sometimes used in pharmacy.

Order 2. Psilotaceae

The only representatives of this order are *Psilotum* (two tropical species) and *Tmesipteris* (one Australian species). They show in some features relationship with the Sphenophyllinae, but are most naturally placed with the Lycopodinae. The complete absence of roots is noteworthy. The simple leaves are alternately arranged on the dichotomous stems; the fertile leaves near the tips of the branches are always deeply divided and resemble a pair of leaves.

Order 3. Selaginellaceae [126]

To this order belongs the genus *Selaginella*, represented by numerous and for the most part tropical species. They have, as a rule, profusely-forked, creeping, and sympodially-branched stems, but occasionally erect branched stems; some form moss-like beds of vegetation; others, climbing on adjacent plants, possess stems several metres long. Certain xerophilous species (*S. lepidophylla* in tropical America, etc.) can endure drying up for months or even years, closing together their rosette-shaped shoots by a cohesion-mechanism, expand again on the arrival of rain [127]. In general the Selaginellas are similar in habit to the Lycopodiums. They have small scale-like leaves which usually exhibit a dorsiventral arrangement, such as is shown, for example, in the alpine *Selaginella helvetica* (Fig. 494), the stem of which bears two rows of small dorsal or upper leaves, and opposite to them two rows of larger, ventral, or under leaves. (Cf. also Fig. 134.) The rhizophores [128] are organs that are peculiar to the plants of this order; they are cylindrical, leafless, shoot-like structures, which arise exogenously, usually in pairs, from the stem at a bifurcation. At their ends a number of endogenous roots are produced, but the rhizophores are able, when the normal shoots are cut back, to continue their growth as shoots of ordinary construction. Even below the first leaves of the seedling plant short rhizophores are formed, from which the first roots arise endogenously. The leaves of *Selaginella* are characterised by the presence at their base on the upper side of a small membranous ligule. This serves as an organ for the rapid absorption of water (rain-drops) by the leafy shoot [129]. In many species of *Selaginella* the epidermal assimilatory cells of the leaves possess, as in *Anthoceros*, only one large chloroplast [130].

The cones or flowers are terminal, simple or branched, radially symmetrical, or less commonly dorsiventral. Each sporophyll subtends only one sporangium, which springs from the stem above the leaf-axil. The same spike bears both macrosporangia and microsporangia. Each macrosporangium (Fig. 495 *A-C*) contains only four macrospores, which are produced by the growth and division of a single spore-mother-cell; all the other mother-cells originally developed ultimately disappear. On account of the increasing size of the spores the spherical macrosporangia become nodular. Opening, which is due to a cohesion-mechanism, occurs along definite lines of dehiscence, the wall splitting into two valves, which curve back from a boat-shaped basal portion. The spores are ejected by the pressure of the contracting boat-shaped part and the valves. Numerous spores are formed in the flattened microsporangia. The mode of dehiscence is similar in these also, but the boat-shaped portion of the wall is smaller, the valves extending to the base.

The microspores begin their development while still enclosed within the

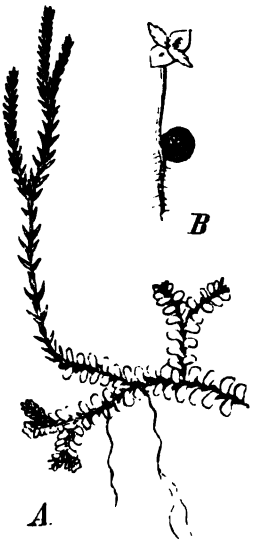


FIG. 494.—*A*, *Selaginella helvetica* (from nature, nat. size). *B*, *Selaginella Kraussiana*, embryonic plant with macrospore still attached. (After BISCHOFF, magnified.)

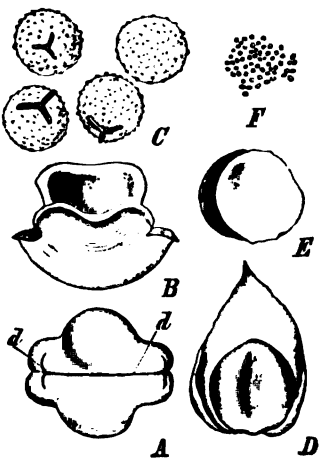


FIG. 495.—*Selaginella helvetica*. *A*, Macrosporangium from above showing the line of dehiscence (*d*). *B*, Opened, seen from the side; the four macrospores, *C*, have been ejected. *D*, Microsporangium in the axil of its sporophyll. *E*, The same, opened. *F*, Microspores. (× about 15.)

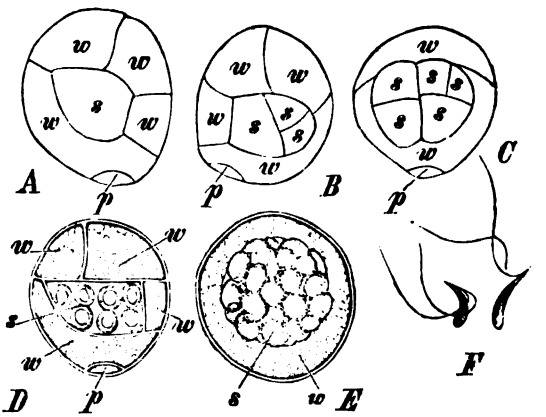


FIG. 496.—*A-E*, *Selaginella stolonifera*, successive stages in the germination of a microspore; *p*, prothallial cell; *w*, wall-cells of antheridium; *s*, spermatogenous cells; *A*, *B*, *D*, lateral, *C*, dorsal view. In *E* the prothallial cell is not visible, the disorganised wall-cells enclose the spermatozoid mother cells; *F*, spermatozoids of *Selaginella cuspidata*. (*A-E* × 640, *F* × 780. After BELAJEFF.)

sporangium. The spore first divides into a small lenticular vegetative cell, which

corresponds to the rhizoid cell of *Salvinia*, and into a large cell, which divides successively into eight sterile prothallial or wall cells and two or four central spermatogenous cells (Fig. 496 *A*). By the further division of the central cells, which represent a single antheridium, numerous spermatozoid mother cells are formed (*B-D*). The peripheral cells then break down and give rise to a mucilaginous substance, in which is embedded the central mass of spermatozoid mother cells (*E*). The small prothallial cell (*p*), however, persists. The whole male prothallium is up to this stage still enclosed by the wall of the microspore. This ultimately ruptures, and the mother cells are set free and liberate the club-shaped spermatozoids. Each of these has two long cilia at its pointed end.

The macrospores in some species similarly begin their development within the sporangia. After the division of the nucleus into daughter-nuclei and their distribution in the apical cytoplasm, the formation of cell walls begins. In this

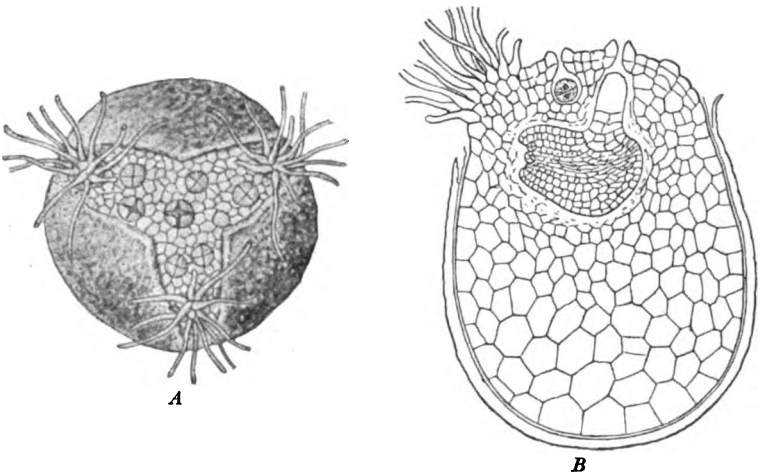


FIG. 497.—*Selaginella Martensii*. *A*, Ruptured macrospore seen from above showing the prothallus with three groups of rhizoids and several archegonia (× 112). *B*, Longitudinal section of the prothallus showing two archegonia in which embryos are developing (× 112). (After BRUCHMANN.)

way, progressing from apex to base, the spore becomes filled by a process of multicellular formation, with large prothallial cells. At the same time, and proceeding in the same direction, there begins a further division of these cells into smaller cells. In some species the apical disc of tissue is formed first, and is separated by a thickened wall or diaphragm from the rest of the cavity of the spore; cell-formation occurs in this later. In the tissue at the apex, consisting of small cells, the rudiments of a few archegonia appear, often even before the formation of the prothallium has been completed. The archegonia are usually not formed until the spores have been discharged from the sporangium, but in some cases even fertilisation takes place on the parent plant.

The wall of the spore eventually bursts at the apex, and the prothallium becomes partially protruded; it forms a number of rhizoids on three projections of its tissue. The fertilisation of one or two archegonia, which then takes place, is followed directly by the segmentation of the fertilised egg-cells and the formation of the embryos (Fig. 497).

The development of the embryo, in which a suspensor consisting of one or several cells, the apex of the stem with the first leaves, the first rhizophore and the foot are distinguishable, proceeds in a great variety of ways in the genus. The first division in the fertilised egg-cell is transverse. In *S. Martensii*, *spinulosa*, *helvetica*, etc., the upper hypobasal cell gives rise to the suspensor only, the main portion of the embryo being derived from the lower cells (Fig. 498); in *S. denticulata* the upper cell forms the foot and rhizophore as well as the suspensor. The apex of the shoot with the first pair of leaves grows upwards and the root downwards; the young plant remains attached to the prothallus in the megaspore by the foot (Fig. 494 *B*). In some species (*S. rubricaulis*, *spinulosa*) the archegonia remain closed and the egg develops apogamously into the embryo. In *S. Kraussiana* and related forms the suspensor, according to Bruchmann, is reduced, but replaced functionally by a special embryonic tube proceeding from the wall of the mother cell of the ovum; the embryo is delimited in this and comes into relation with the nutritive tissue.

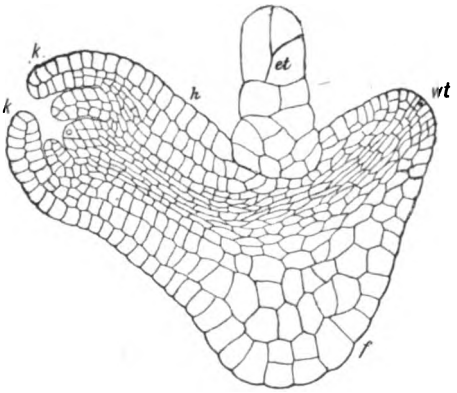


FIG. 498.—*Selaginella Martensii*. Embryo before becoming free from the prothallus in longitudinal section; *f*, foot; *wt*, rhizophore; *et*, suspensor; *k*, cotyledons with their ligules. (× 150. After BRUCHMANN.)

Order 4. Isoetaceae [121]

The isolated genus *Isoetes* must be regarded as a persistent branch of an ancient group of plants, which in earlier geological periods was more richly represented. The species of *Isoetes* are perennial plants, growing either on damp soil or submerged in water. The stem is short and tuberous, rarely dichotomously branched, terminating below in a tuft of dichotomously-branching roots, and above in a thick rosette of long, stiff, awl-shaped leaves (Fig. 499). The stem is characterised by a secondary growth in thickness by means of a cambium; this produces to the outer side cortex (without phloem) and to the inner side secondary phloem and xylem. The leaves are traversed longitudinally by four air-passages, and expand at the base into a broad sheath. On the inner side of the leaves, above their point of insertion, is an elongated pit, the fovea, containing a large sessile sporangium. A ligule, in the form of a triangular membrane, is inserted above the fovea. *Isoetes* thus differs greatly in habit from the other genera, but resembles *Selaginella* in the development of a ligule. On this account *Isoetes* and *Selaginella* are termed Ligulatae; the extinct Sigillariaceae and Lepidodendraceae also belong to this group.

The macrosporangia are situated on the outer leaves of the rosette; the microsporangia on the inner. Both are traversed by transverse plates of tissue or trabeculae, and are in this way imperfectly divided into a series of chambers. In contrast to *Selaginella* numerous macrospores are formed in each macrosporangium. The spores are set free by the decay of the sporangial walls.

The development of the sexual generation is accomplished in the same way as in *Selaginella*. The reduced male prothallium (Fig. 500) arises similarly within

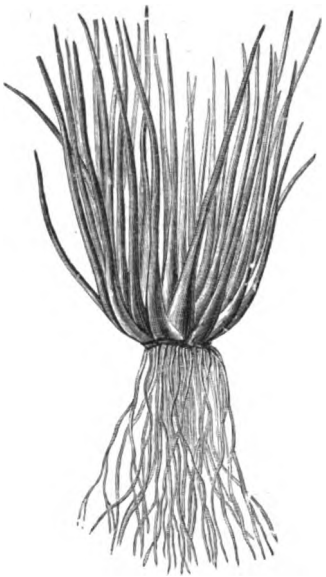


FIG. 499.—*Isoetes lacustris*. (½ nat. size.)

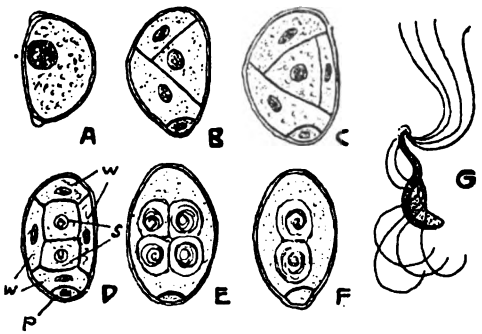


FIG. 500.—*A-F*, *Isoetes setacea* (× 640). *A*, Microspore seen from the side. *B-D*, Segmentation of the spore; *p*, prothallial cell; *w*, the four cells of the wall; *s*, spermatogenous cells. *E*, The four spermatozoid mother cells are surrounded by the disorganised cells of the wall; surface view. *F*, The same in side view. *G*, *Isoetes Malinverniana*, spermatozoid (× 780). (After BELAJEFF.)

the spore, by the formation of a small, lenticular, vegetative cell (*p*), and a larger cell, the rudiment of a single antheridium. The larger cell divides further into

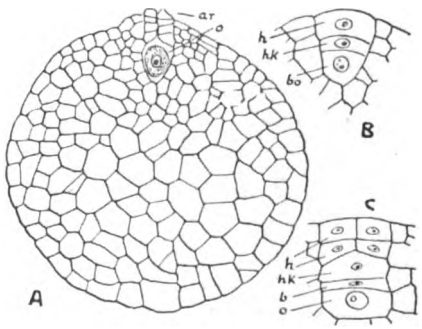


FIG. 501.—*Isoetes echinospora*. *A*, Female prothallium; *ar*, archegonium; *o*, egg-cell. *B*, *C*, Development of the archegonium from a superficial cell; *h*, neck-cells; *hk*, neck-canal-cell; *b*, ventral canal-cell; *o*, egg-cell. (× 250. After CAMPBELL.)

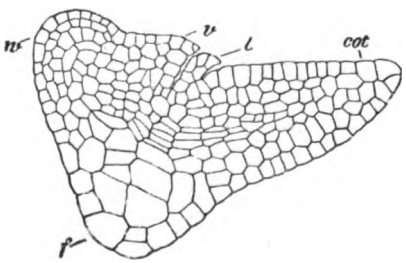


FIG. 502.—*Isoetes echinospora*. Embryo before breaking out from the prothallus in longitudinal section; *cot*, cotyledon; *l*, ligule; *v*, sheath at the base of the cotyledon in the axil of which the apex of the stem arises; *w*, root; *f*, foot. (× 200. After CAMPBELL.)

four sterile peripheral cells, which completely enclose two central spermatogenous cells. From each of the latter arise, in turn, two spermatozoid mother cells, four in all, each of which, when liberated by the rupture of the spore wall, gives rise

to a single, spirally-coiled, multiciliate spermatozoid. The female prothallium (Fig. 501), just as in *Selaginella*, also remains enclosed within the macrospore, and is incapable of independent growth. It shows similarly an approach to the Conifers, in that the nucleus first divides into numerous, parietal daughter-nuclei before the gradual formation of the cell walls, which takes place from the apex of the spore to the base. As a result of this process the whole spore becomes filled with a prothallium, at the apex of which the archegonia are developed. The embryo (Fig. 502) has no suspensor and thus differs from other Lycopodinae.

Order 5. Sigillariaceae [132]

The Sigillarias, found from the Culm onwards, are most numerous in the Carboniferous period, and persist to the Bunter Sandstone. They were stately

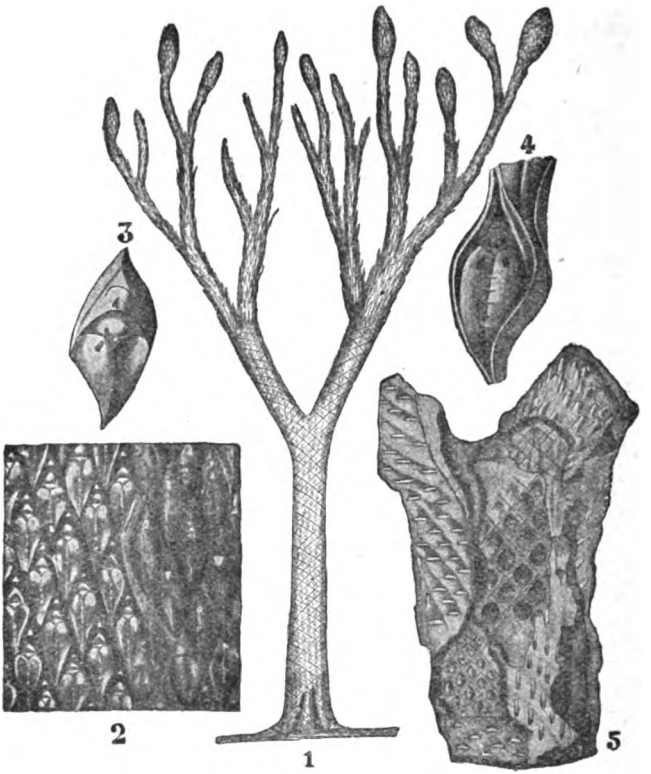


FIG. 503.—*1*, *Lepidodendron*. Reconstruction (after POTONIÉ). *2*, *L. Aculeatum*, cast of stem surface (after STERNBERG). *3*, *4*, *Lepidodendron*, leaf-cushions (after POTONIÉ). *5*, Piece of cortex (after SEWARD). (From LOTSY, *Botan. Stammesgeschichte*.)

trees, with but little-branched, pillar-like stems, which grew in thickness. They had long narrow leaves with a ligule, which when they fell off left longitudinal rows of hexagonal leaf-scars on the surface of the stem. Long-stalked, cone-

like flowers were borne on the stem; the sporangia were borne singly on the sporophylls. Heterosporous.

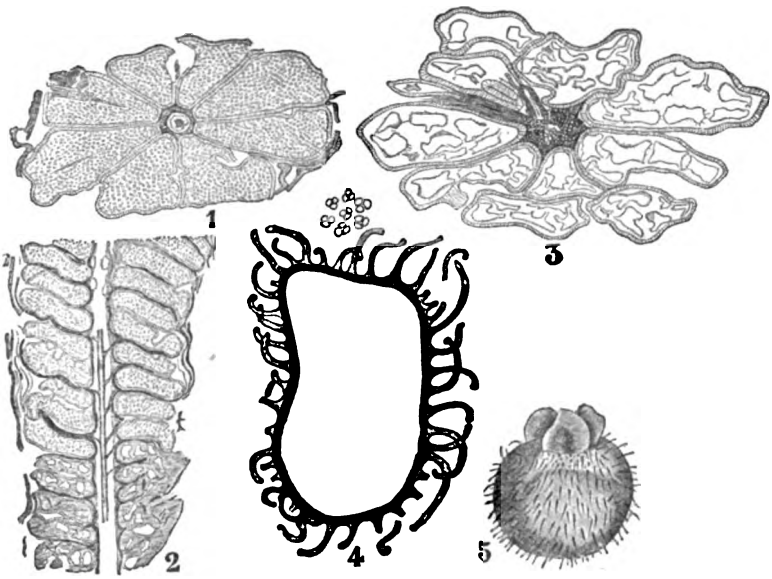


FIG. 504.—*Lepidostrobus Veltheimianus*. *1*, Transverse section of cone with microsporangia; tetrads to right below. *2*, Cone in longitudinal section showing microsporangia above and macrosporangia below. *3*, Transverse section of cone with macrosporangia. *4*, Macrospore in longitudinal section. *5*, Macrospore, probably opening in course of germination. (*1-5* after SCOTT, KIDSTON, BINNEY.) From LOTSY.

Order 6. Lepidodendraceae [122, 133]

The Lepidodendrons extend from the Devonian to the Rothliegende, but are best developed in the Carboniferous period. They were tree-like plants attaining a height of some 30 metres with dichotomously-branched stems which grew in thickness. The leaves, which attained a length of 15 cm., were spirally arranged and seated on rhombic leaf-cushions (Fig. 503). The cone-like flowers (*Lepidostrobus*) were borne on the ends of branches or sprang from the stem itself; each sporophyll bore a single sporangium, which contained either macrospores or microspores (Fig. 504). The number of spores in the macrosporangium was larger than in *Selaginella*. A prothallus was formed in the spore and resembled that of the existing genus.

The discovery of seed-like structures borne by some of the palaeozoic Lycopodinae (*Lepidocarpon*, *Miadesmia*) is of special interest. In them the macrosporangium was surrounded by an integument leaving only a narrow slit-like opening; the sporophyll also took part in enclosing the sporangium. Only one macrospore attained full development. As in *Isoetes* the prothallium remained within the spore. The macrospores were produced on sporophylls resembling those of *Lepidostrobus*. Probably pollination occurred while the

sporangia was still attached to the parent plant from which later the macrosporophyll, together with its sporangium, separated as a whole.

Fig. 505.—*Lyginodendron.* Frond. (*Sphenopteris Hoeninghousii.*) (Reduced ½. After Potonié.)

Class V

Pteridospermeae [132, 134]

So far as our knowledge goes the Equisetinae, Sphenophyllinae, and Lycopodinae are branches of the Pteridophyte stock which have undergone no further development in the direction of the more highly organised plants. From the Filicinae, on the other hand, the first seed-plants had arisen even in palaeozoic times. These are the Pteridospermeae, which stand on a higher level than all other Pteridophytes and connect the Ferns with primitive Gymnosperms

(Cordaiteae, Cycadeae); they have thus great importance in the

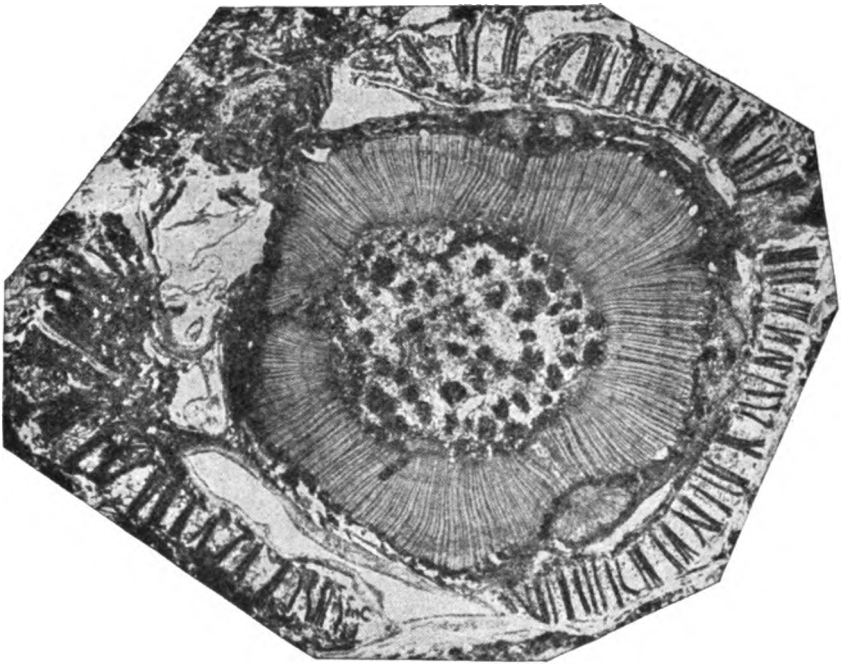


FIG. 506.—*Lyginodendron oldhamium.* Transverse section of stem. (× 2½. After SCOTT.)

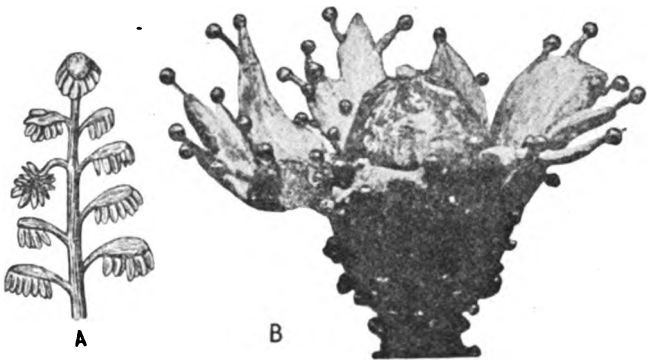


FIG. 507.—*Lyginodendron oldhamium.* *A*, Microsporangia (*Crossotheca*). *B*, Macrosporangium (*Lagenostoma*). Reconstruction. The open cupule bears stalked glands. (After SCOTT.)

phylogeny of the higher plants. They became extinct in the Permian period.

In their vegetative organs the Pteridosperms resembled especially the

Marattiaceous ferns. Their fronds (*Sphenopteris*, Fig. 505; *Neuropteris*) were highly compound, the main rachis dividing dichotomously above the base. The stem had axillary branching (*Lyginodendron*) and underwent secondary thickening by means of a cambium; this cut off radially-seriated xylem elements to the inside and phloem to the outside (Fig. 506). The leaf-trace bundles met with in the cortex traverse the zone of wood to unite with the strands of primary xylem at the periphery of the pith. The roots also underwent secondary thickening.

The Pteridosperms were heterosporous; the sporangia were borne on fronds that resembled those of ordinary ferns. The microsporangia (*Crossotheca*, Fig. 507 *A*) showed resemblances to Marattiaceae; the macrosporangia (*Lagenostoma*, Fig. 507 *B*), on the other hand, were surrounded by a cupule and resembled in construction the ovules of the Cycadeae; the macrosporophylls were not, however, arranged in cones.

DIVISION II

SPERMATOPHYTA

DIVISION II

SPERMATOPHYTA

The Transition from the Pteridophyta to the Spermatophyta [1].—The Pteridophyta are characterised by the type of alternation of generations they exhibit. The spore gives rise to the independently living, haploid gametophyte. This is the short-lived prothallus, from the fertilised egg-cell of which the physiologically independent diploid sporophyte arises and forms the Fern, Horse-tail, or Club-moss. The appearance of heterospory leads to a further reduction of the prothallus, which ceases to produce both kinds of sexual organs. In the germination of the microspores only a single, vegetative prothallium-cell is to be recognised, the remainder of the small prothallium representing one or more antheridia. The female prothallium, which in *Salvinia* still becomes green and emerges from the macrospore, in *Selaginella* and *Isoetes* has lost the power of independent nutrition. The prothallium begins its development while still within the macrosporangium of the parent plant, and the macrospore, after being set free, only opens in order to allow of the access of the spermatozoids to the archegonia. From the fertilised egg the embryo develops without a resting period into the young sporophyte.

The simplest Spermatophyta are only distinguished by inessential differences from these most highly differentiated Archegoniatae.

The MACROSPORE, which in the Spermatophyta is termed the EMBRYO-SAC, remains enclosed in the MACROSPORANGIUM or OVULE (Fig. 508). The latter consists of the NUCELLUS (*n*), from the base of which (the CHALAZA (*ch*)) one or two INTEGUMENTS (*ii*, *ia*) arise; these grow up as tubular investments of the nucellus and only leave a small passage, the MICROPYLE (*m*), leading to the tip of the latter. The ovule is attached to the MACRO-SPOROPHYLL or CARPEL by a stalk or FUNICULUS (*f*), which is often very short. The region to which one or more ovules are attached is called the PLACENTA. If the nucellus forms the direct continuation of the funiculus the ovule is termed straight or ATROPOUS. More frequently the funiculus is sharply curved just below the chalaza, so that the ovule is bent back alongside its stalk (ANATROPOUS ovule). The line of junction of the funiculus

with the outer integument is still recognisable in the ripe seed, and is termed the RAPHE. Lastly the ovule itself may be curved, in which case it is spoken of as CAMPYLOTROPOUS. The three types are diagrammatically represented in Fig. 508 *A-C*.

As a rule only one embryo-sac is contained in an ovule. In the same way as the four macrospores originate by the tetrad division in the macrosporangium of *Selaginella*, in the macrosporangium (ovule) of the Spermatophyta there is usually a single embryo-sac mother cell which divides into four daughter cells; three of these do not develop further, while the fourth becomes the embryo-sac. The embryo-sac of the simplest Spermatophyta also resembles the macrospore in becoming filled with prothallial tissue, here termed the endosperm; one or more archegonia with large egg-cells are developed at the summit of this. The fertilised ovum develops into the embryo while

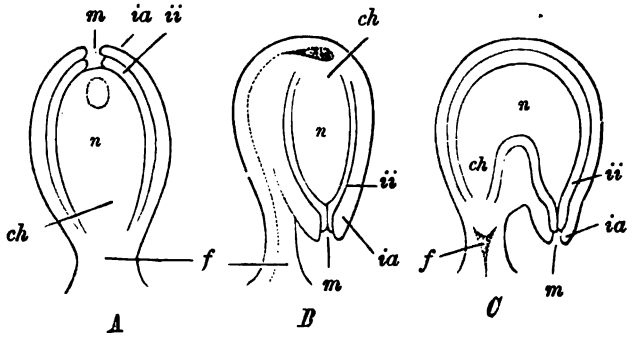


FIG. 508.—*A*, Atropous; *B*, anatropous; *C*, campylotropous ovules. Diagrammatic and magnified. Modified from SCHIMPER. Description in the text.

still enclosed within the macrospore and at the expense of the parent plant. When the embryo has reached a certain stage in its development, which is different and characteristic in different plants, its growth is arrested, and after the separation from the parent plant it undergoes a period of rest. It is still surrounded by the other portions of the macrosporangium, viz. the prothallium or endosperm, the nucellus (if this still persists), and the seed coat formed from the integuments. THE COMPLETE STRUCTURE DERIVED FROM THE OVULE IS TERMED A SEED, AND THE FURTHER DEVELOPMENT OF THE UNOPENED MACROSPORANGIUM TO FORM A SEED, THE FIRST ORIGIN OF WHICH WAS SEEN IN THE PTERIDOSPERMEAE (p. 534), IS CHARACTERISTIC OF ALL SEED-PLANTS OR SPERMATOPHYTA.

The MICROSPORES of the Spermatophyta are called POLLEN GRAINS. They are formed in large numbers within the MICROSPORANGIA or POLLEN SACS, which are borne singly or in numbers on the MICROSPOROPHYLLS or STAMENS. The part of the stamen which bears the pollen sacs is usually clearly distinguishable and is called the ANTHER.

The development of the pollen sac (Fig. 509) commences with divisions parallel to the surface taking place in cells of the hypodermal layer; this separates the cells of the primary archesporium from an outer layer of cells. The latter divides to form three layers of cells. The outermost layer of the wall in Gymnosperms and the hypodermal layer in the Angiosperms gives rise to the fibrous layer and the innermost layer to the tapetum. The archesporium after undergoing a number of divisions forms the pollen-mother-cells, each of which divides as in Bryophytes and Pteridophytes into four daughter cells. These

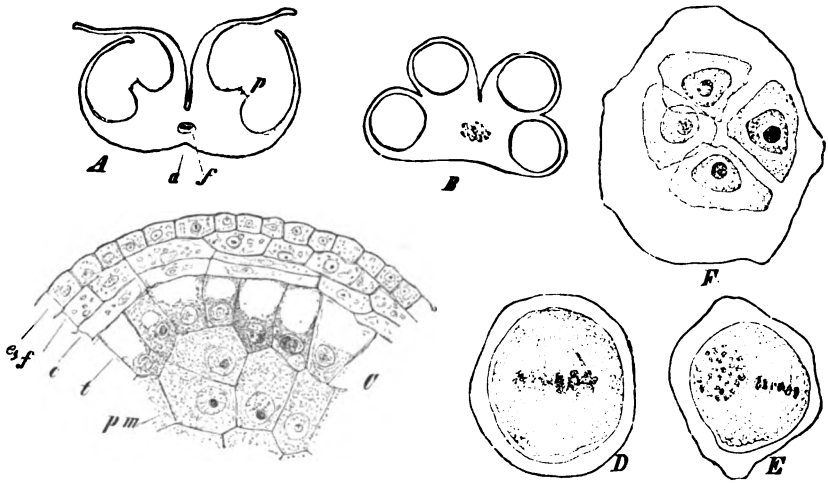


FIG. 509.—*Hemerocallis fulva*. *A*, Transverse section of an almost ripe anther, showing the loculi ruptured in cutting; *p*, partition wall between the loculi; *a*, groove in connective; *f*, vascular bundle (× 14). *B*, Transverse section of young anther (× 28). *C*, Part of transverse section of a pollen sac; *pm*, pollen-mother-cells; *t*, tapetal layer, later undergoing dissolution; *c*, intermediate parietal layer, becoming ultimately compressed and disorganised; *f*, parietal layer of eventually fibrous cells; *e*, epidermis (× 240). *D* and *E*, Pollen-mother-cells of *Alchemilla speciosa* in process of division (× 1125). *F*, Mature tetrad of *Bryonia dioica* (×800). (After STRASBURGER).

are the pollen grains, and are spherical or ellipsoidal in shape and provided with a cell wall; an external cutinised layer (the EXINE), and an inner cellulose layer, rich in pectic substances (the INTINE), can be distinguished in the wall.

While the male sexual cells of all archegoniate plants are dependent on water for their conveyance to the female organs, the transport of the pollen grains to the egg-cells is brought about in Spermatophytes by means of the wind or by animals. However far the reduction of the male prothallium has proceeded—and even in the case of the heterosporous Pteridophyta only a single sterile cell was present—two constituent parts are always distinguishable in the germinating pollen grain; these are a VEGETATIVE CELL which grows out as the POLLEN-

TUBE, and an ANTHERIDIAL MOTHER CELL which ultimately gives rise to two GENERATIVE CELLS. The pollen-tube, the wall of which is continuous with the intine of the pollen grain, ruptures the exine and penetrates, owing to its chemotropic irritability, into the tissue of the macrosporangium (cf. p. 352). The antheridial mother cell passes into the pollen-tube and sooner or later gives rise to two generative cells which reach the embryo sac and egg-cell by passing along the pollen-tube. The name Siphonogams has been applied to the seed-plants on account of the common character of the group afforded by the formation of a pollen-tube.

The results reached by the above survey may be summarised by saying that the Phanerogams continue the series of the Archegoniatae and agree with the latter in exhibiting an alternation of generations (cf. the Scheme on p. 543). While the asexual generation becomes more complex in form and more highly organised, there is a corresponding reduction of the sexual generation. The female sexual generation is enclosed, throughout its whole development, in the asexual plant, and only becomes separated from the latter in the seed, which further contains as the embryo the commencement of the succeeding asexual generation.

The investigations made of recent years into the phenomena of the reduction division (cf. p. 204) in the spore-mother-cells of Archegoniates and Spermatophyta have resulted in a confirmation of the limits of the two generations in the latter (2). The number of chromosomes characteristic of any plant is diminished to one-half, during the divisions that lead to the origin of the sexual generation, and the full number of chromosomes is not again attained until fertilisation takes place. The asexual generation has always the double number, the sexual generation the single number of chromosomes. The gametophyte is haploid, the sporophyte diploid.

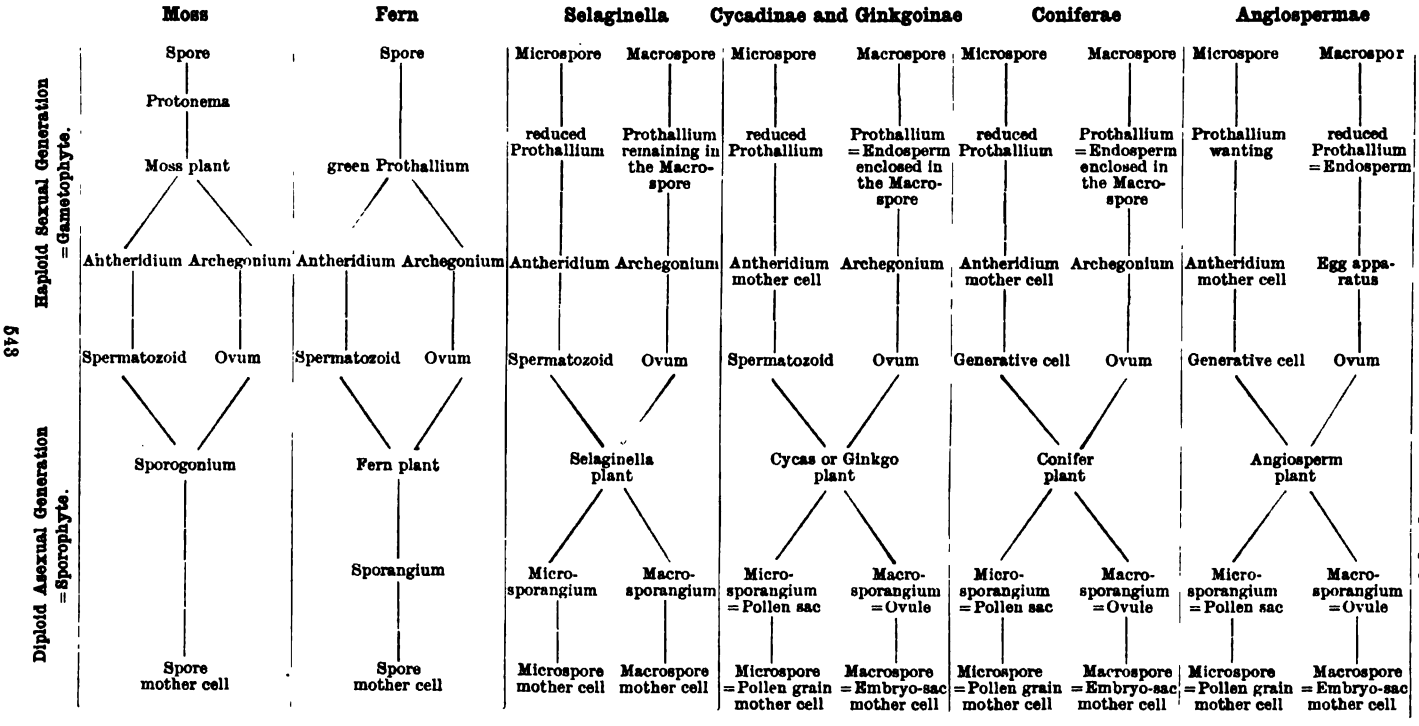
The Spermatophyta are divided into two classes which differ in their whole construction: (1) the Gymnosperms, with naked seeds; (2) the Angiosperms, with seeds enclosed in an ovary.

The names of these classes indicate the nature of one of the most important differences between them. THE CARPELS OF THE ANGIOSPERMS FORM A CLOSED CAVITY, THE OVARY, WITHIN WHICH THE OVULES DEVELOP. SUCH AN OVARY IS WANTING IN THE GYMNOSPERMS, THE OVULES OF WHICH ARE BORNE FREELY EXPOSED ON THE MACROSPOROPHYLLS OR CARPELS.

The Gymnosperms are the phylogenetically older group. Their construction is simpler and in the relations of their sexual generation they connect directly with the heterosporous Archegoniatae; they might indeed be treated as belonging to this group.

The Angiosperms exhibit a much wider range in their morphological and anatomical structure. The course of their life-history differs considerably from that of the Gymnosperms, and without the

Scheme of Alternation of Generations



intermediate links supplied by the latter group the correspondence with the life-history of the Archegoniatae would not be so clearly recognisable.

These conclusions are confirmed by the evidence afforded by Palaeobotany. Gymnosperms or forms resembling them are found along with what appear to be intermediate forms between the Gymnosperms and the Pteridophyta in the fossiliferous rocks of the Devonian, Carboniferous, and Permian formations. The Angiosperms are, on the other hand, first known from the Cretaceous formation.

Morphology and Ecology of the Flower (3)

1. Morphology.—The flowers of the **Gymnosperms** are all unisexual and diclinous. The macrosporophylls form the female, the

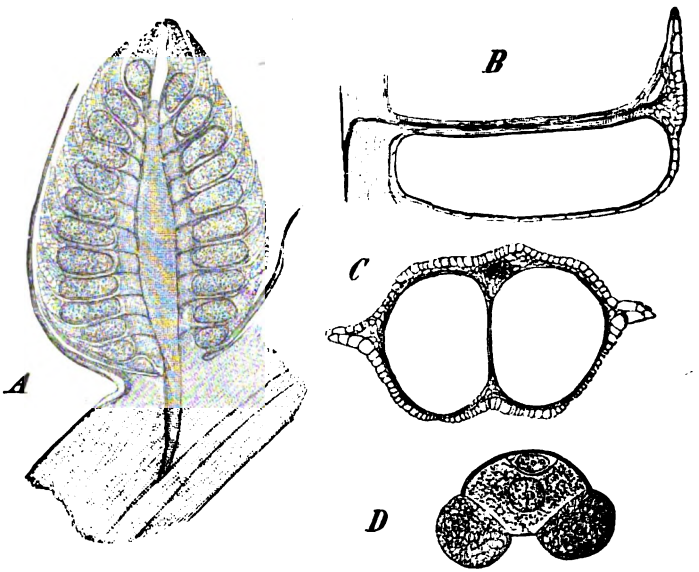


FIG. 510.—*Pinus montana*. *A*, Longitudinal section of a ripe male flower (× 10). *B*, Longitudinal section of a single stamen (× 20). *C*, Transverse section of a stamen (× 27). *D*, A ripe pollen grain of *Pinus sylvestris* (× 400). (After STRASBURGER.)

microsporophylls the male flowers. The two sexes are found either on the same individual (MONOECIOUS), or each plant bears either male or female flowers (DIOECIOUS). Leaves forming an envelope around the group of sporophylls are only found in a few flowers of the Gymnospermae (Gnetaceae).

The MALE FLOWERS are shoots of limited length, the axis of which bears the closely crowded and usually spirally arranged sporophylls. The scales which invested the flower in the bud often persist at the

base of the axis (Fig. 510). The microsporangia are borne on the lower surface of the sporophylls, two or more being present on each. Their opening is determined as in the sporangia of the Pteridophyta by the peculiar construction of the outer layer of cells of the wall (exothecium). The pollen grains are spherical, and are frequently provided with two sacs filled with air, which increase their buoyancy and assist in their distribution by the wind (Fig. 510). On germination the outer firm layer of the wall of the pollen grain (exine) is completely lost, being fractured by the increase in size of the protoplasmic body.

In many Gymnosperms the FEMALE FLOWERS or CONES resemble the male flowers in being composed of an axis bearing numerous spirally-arranged sporophylls. In other cases they differ from this type in various ways, which will be described below (pp. 589 ff.).

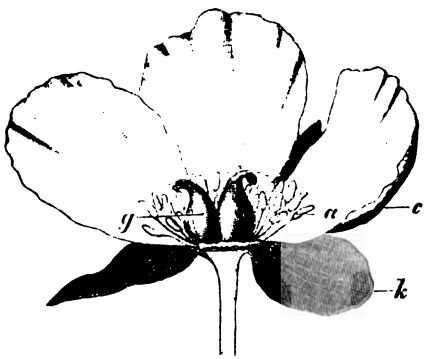


FIG. 511.—Flower of *Paeonia peregrina*, in longitudinal section. *k*, Calyx, and *c*, corolla, together forming the perianth; *a*, androecium; *g*, gynaeceum. The anterior portion of the perianth has been removed. (½ nat. size. After SCHENCK.)

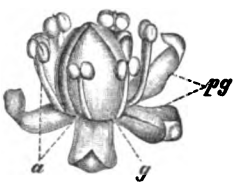


FIG. 512.—Flower of *Acorus Calamus*. *pg*, Perigone; *a*, androecium; *g*, gynaeceum. (Enlarged. After ENGLER.)

In **Angiosperms**, on the other hand, a union of micro- and macrosporophylls in the one flower, which is thus HERMAPHRODITE, and the investment of the flower by coloured leaves (differing in appearance from the foliage leaves), forming a PERIANTH, is the rule (Figs. 511, 512). The Quercifloræ afford an example of an exception to these statements. In contrast to the UNISEXUAL or DICLINOUS flower with the sporophylls arranged spirally on an elongated axis, which is characteristic of the Gymnosperms, the perianth leaves and sporophylls in the Angiosperms are usually borne in whorls on a greatly shortened axis. THE ARRANGEMENT OF THE FLORAL LEAVES IN WHORLS, THE COLOURED PERIANTH, AND THE HERMAPHRODITE NATURE OF THE FLOWERS ARE THUS CHARACTERISTIC OF ANGIOSPERMS, although these features do not apply without exceptions to all angiospermic flowers. These differences depend on the important factor of the MEANS OF POLLINATION. When, as is the case with the Gymnosperms

and the catkinate flowers of Angiosperms, this function is performed by the wind, the elongation of the axis and the absence of an investment of leaves around the female receptive organ are advantageous. When, on the other hand, pollination is effected by insects or birds, the conspicuousness given by the presence of a perianth and other attractions, such as scent or sweet-tasting substances, are necessary. The form of the flower, the arrangement of the sporophylls in it, and the place at which nectar is secreted must be adapted to the body-form or the habits of the visiting animals. It is to this that the variety of form and colour exhibited in the flowers of Angiosperms must be ascribed.

The association of hermaphrodite and unisexual flowers on the same plant leads in certain Angiosperms to what is known as POLYGAMY. When hermaphrodite and unisexual flowers are distributed on distinct individuals we have andro- or gyno-dioecism; when on the same individual andro- or gyno-monoecism.

The perianth usually consists of two whorls of members: these may be similar in form and colour (*e.g. Lilium*), when the name PERIGONE is given to them, or may be differentiated into an outer green CALYX and an inner whorl of coloured leaves, the COROLLA (*e.g. Rosa*). In every complete flower two whorls of stamens or microsporophylls come next within the perianth, and within these again a whorl of carpels or macrosporophylls. The whorls alternate regularly with one another. The stamens collectively form the ANDROECIUM, the carpels the GYNAECEUM.

Each stamen consists of a cylindrical stalk or FILAMENT and of the ANTHER; the latter is formed of two THECAE or pairs of pollen-sacs joined by the continuation of the filament, the CONNECTIVE (Fig. 513). According to whether the thecae are turned inwards, *i.e.* towards the whorl of carpels, or outwards, the anther is described as INTRORSE or EXTRORSE. The opening of the ripe theca depends as a rule (except in the Ericaceae) on the peculiar construction of the hypodermal layer of the wall of the pollen sac. This is called the fibrous layer or ENDOTHECIUM. On the other hand, in the Gymnosperms (excluding *Ginkgo*, cf. p. 591), as in the Ferns, the dehiscence is effected by means of the external layer of cells (exothecium) (p. 545). As a rule the septum between the two pollen sacs breaks down, so that they are both opened by the one split in the wall (Fig. 509 *A*). The microspores in anemophilous plants are smooth, dry, and light, and adapted for distribution by the wind. In entomophilous flowers, on the other hand, the exine is frequently sticky or provided with spiny projections, and the pollen grains are thus enabled to attach themselves better to the bodies of the insect visitors. They also differ from the pollen grains of the Gymnosperms in having more or less numerous spots in the wall prepared beforehand for the emission of the pollen-tube (Fig. 514). Sterile stamens which do not produce fertile pollen are termed STAMINODES.

The flower is terminated above by the GYNAECEUM. The CARPELS composing this may remain free and each give rise to a separate fruit

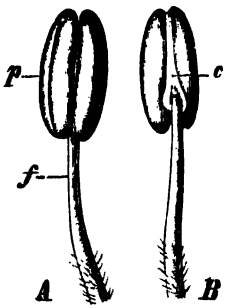


FIG. 513.—*A* and *B*, Anterior and posterior view of a stamen of *Hyoscyamus niger*; *f*, the filament; *p*, anther; *c*, connective (magnified). (After SCHIMPER.)

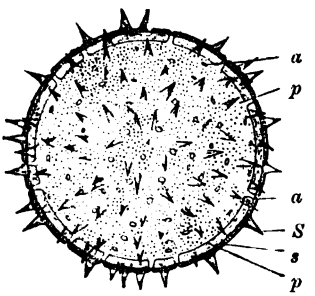


FIG. 514.—Pollen grain of *Malva sylvestris*. *S*, Spinous projections of the exine; *s*, vertically striated layer of the exine; *p*, the same seen from above; *a*, places of exit of pollen-tubes. (After A. MEYER.)

(APOCARPOUS GYNAECEUM) (Figs. 515*a*, 517 *A*), or they unite together to form the ovary (SYNCARPOUS GYNAECEUM) (Fig. 515*b*). The carpels, as a rule, bear the ovules on their margins, on more or less evident outgrowths which are termed PLACENTAS (Fig. 515*a*, *p*). In apocarpous gynaecea the ovules are thus borne on the

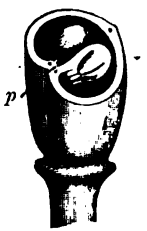


FIG. 515*a*. — *Delphinium consolida*. Cross-section of the ovary, showing the ovules on the placenta (*p*). (After ENGLER and PRANTL.)

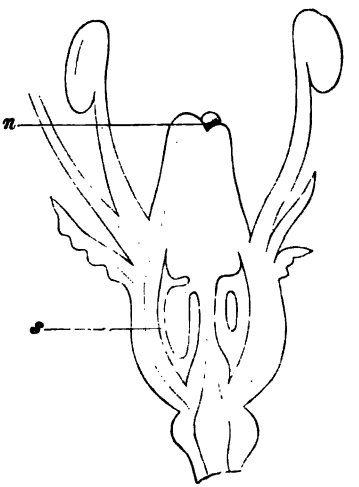


FIG. 515*b*.—*Sambucus nigra*. Longitudinal section of flower. *s*, Ovule; *n*, stigma. (After TSCHIRCH-ÖSTERLE.)

united margins of the carpels, each margin bearing a row of ovules. This is termed the VENTRAL SUTURE, while the midrib of the carpel forms the DORSAL SUTURE. In syncarpous ovaries the ovules are similarly borne on the margins of the coherent carpels (Fig. 516 *pl*).

The placentation is termed PARIETAL when the placentas form projections from the inner surface of the wall of the ovary (Fig. 516 *D*). If the margins of the carpels project farther into the ovary, and divide its cavity into chambers or loculi, the placentas are correspondingly altered in position, and the placentation becomes AXILE (Fig. 516 *B*). In contrast to such TRUE SEPTA, formed of the marginal portions of the carpels, those that arise as outgrowths of the surface or

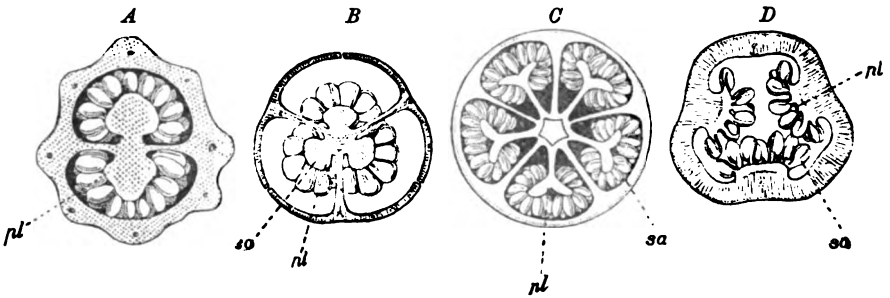


FIG. 516.—Transverse sections of ovaries. *A*, *Lobelia*; *B*, *Diapensia*; *C*, *Rhododendron*; *D*, *Passiflora*; *pl*, placenta; *sa*, ovules. (After LE MAOUT and DECAISNE.)

sutures of the carpels, as in the Cruciferae, are called FALSE SEPTA (Fig. 656). By the upgrowth of the floral axis in the centre of the ovary what is known as FREE CENTRAL PLACENTATION comes about (*e.g.* Primulaceae). The projecting axis cannot be sharply distinguished from the tissue of the carpels. The septa, which were originally present, are arrested at an early stage of development or completely disappear, so that the ovules are borne on the central axis covered with carpellary tissue and enclosed in a wall formed by the outer portions of the carpels.

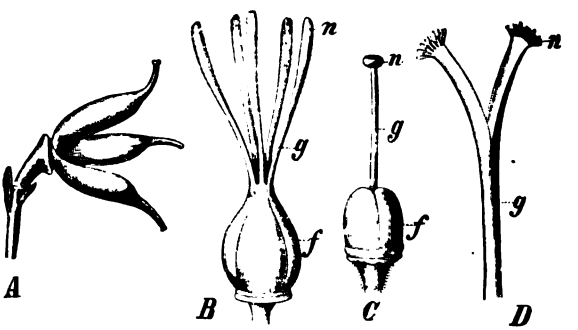


FIG. 517.—Different forms of gynaecea. *A*, Of *Aconitum Napellus*; *B*, of *Linum usitatissimum*; *C*, of *Nicotiana rustica*; *D*, style and stigma of *Achillea millefolium*; *f*, ovary; *g*, style; *n*, stigma. (After BERG and SCHMIDT, magnified.)

Each carpel in an apocarpous gynaeceum is usually prolonged above into a stalk-like STYLE terminating in a variously-shaped STIGMA. The stigma serves as the receptive apparatus for the pollen, and in relation to this is often papillate or moist and sticky (Fig. 517 *D*). When

the gynaeceum is completely syncarpous, it has only one style and stigma. In Fig. 517 an apocarpous (*A*) and a syncarpous gynaeceum (*C*) are represented, together with one in which the carpels are coherent below to form the ovary while the styles are free (*B*).

The POSITION OF THE OVULES WITHIN THE OVARY may be erect,

FIG. 518. — Ovary of *Conium maculatum* with pendulous ovules, in longitudinal section. Raphe ventral. (After TSCHIRCH-ÖSTERLE.)

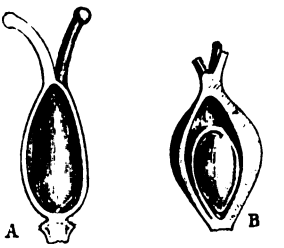


FIG. 519.—Ovaries containing basal ovules shown in longitudinal section. A, *Fagopyrum esculentum* (atropous); B, *Armeria maritima* (anatropous). (× 20. After DUCHARTRE.)

pendulous, horizontal, or oblique to the longer axis (Figs. 518, 519). In anatropous ovules the raphe is said to be ventral when it is turned towards the ventral side of the carpel, and dorsal if towards the dorsal side of the carpel.

The differences in the form of the floral axis, which involve changes in the position of the gynaeceum, lead to differences in the form of the flower itself. Some of the commonest cases are diagrammatically represented in Fig. 520 *A-C*. The summit of the floral axis is usually

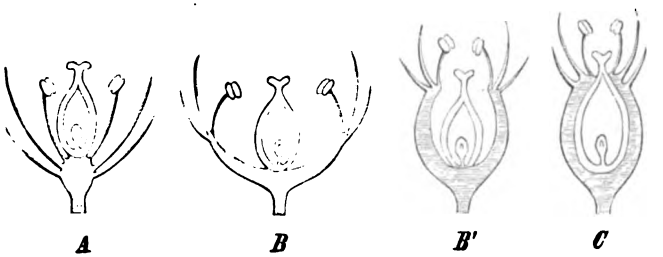


FIG. 520.—Diagram of (*A*) hypogynous, (*B*, *B'*) perigynous, and (*C*) epigynous flowers. (After SCHIMPER.)

thicker than the stalk-like portion below; it is often widened out and projecting, or it may be depressed and form a cavity. If the whorls of members of the flower are situated above one another on a simple, conical axis, THE GYNAECEUM FORMS THE UPPERMOST WHORL AND IS SPOKEN OF AS SUPERIOR, WHILE THE FLOWER IS TERMED

HYPOGYNOUS (Fig. 521, 1). If, however, the end of the axis is expanded into a flat or cup-shaped receptacle (hypanthium), an interval thus separating the androecium and gynaeceum, the flower is termed PERIGYNOUS (Figs. 520 *B*, *B'*, 521, 2). When the concave floral axis, the margin of which bears the androecium, becomes adherent to the gynaeceum, the latter is said to be INFERIOR, while the flower is described as EPIGYNOUS (Fig. 521, 3).

The regions of the axis, or of other parts of the flower which excrete a sugary solution to attract the pollinating animal visitors, are called NECTARIES. Their ecological importance is considerable.

In a typical angiospermic flower the organs are thus arranged in five alternating whorls, of which two comprise the perianth, two the androecium, while the gynaeceum consists of one whorl. The flower is PENTACYCLIC. The number of members is either the same in each

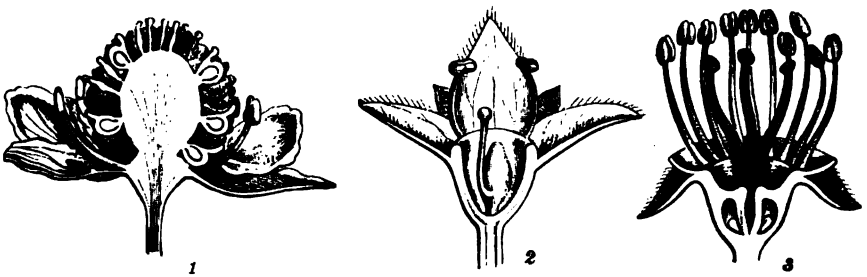


FIG. 521.—Flowers in longitudinal section. *1*, *Ranunculus sceleratus* with numerous apocarpous carpels on a club-shaped receptacle; hypogynous flower. (After BAILLON, magnified.) *2*, *Alchemilla alpina*, perigynous; *3*, *Pyrus Malus*, epigynous. (After FOCKE in *Nat. Pflanzenfamilien*, magnified.)

whorl (*e.g.* three in a typical Monocotyledon flower, or five in a typical Dicotyledon flower), or an increase or decrease in the number takes place. This is especially the case with the whorls composing the androecium and gynaeceum. Further, as is shown in the androecium, a whorl may be entirely omitted or the number of whorls may be increased. Flowers with only one whorl in the androecium are termed haplostemonous, and those with two whorls diplostemonous. When the outer whorl of the androecium (and in correspondence with this the carpels) does not alternate with the corolla but falls directly above this, the androecium is obdiplostemonous.

A diagram (cf. p. 88) of a pentacyclic Monocotyledon flower, so oriented that the cross-section of the axis of the inflorescence stands above and that of the subtending bract (cf. p. 121) below, is given in Fig. 522, and that of a Dicotyledon flower in Fig. 523.

Both these floral diagrams are spoken of as empirical diagrams. A theoretical diagram, on the other hand, is obtained when not only the organs actually present are represented but also others the former presence of which must be

assumed on phylogenetic grounds. Thus in the Iridaceae, which are closely related to the Liliaceae, only one whorl of stamens (the outer) is present; the inner whorl which might have been expected has been lost (Fig. 524). When the position of the missing members is marked by crosses in the empirical diagram the theoretical floral diagram of the Iridaceae is obtained.

A FLORAL FORMULA gives a short expression for the members of a flower as shown in the floral diagram. Denoting the calyx by K, the corolla by C (if the perianth forms a perigone it is denoted by P), the androecium by A, and the gynaeceum by G, the number of members in each case is placed after the letter. When there is a large number of members in a whorl the symbol ∞ is used, denoting that the number is large or indefinite. Such a formula may be further made to denote the cohesion of the members of a whorl by enclosing the proper number within brackets; by placing a horizontal line below or above the number of the carpels the superior or inferior position of the ovary is expressed.

FIG. 522.—Diagram of a pentacyclic monocotyledonous flower (*Lilium*). (After SCHENCK.)

FIG. 523.—Diagram of a pentacyclic dicotyledonous flower (*Viscaria*). (After EICHLER.)

FIG. 524.—Theoretical diagram of the flower of *Iris*. The missing whorl of stamens is indicated by crosses. (After SCHENCK.)

The floral diagrams in Figs. 522 and 523 would be expressed respectively by the floral formulae, P3+3, A3+3, G(3) for the Monocotyledon, and K5, C5, A5+5, G(5) for the Dicotyledon. Other examples are *Ranunculus*, K5, C5, A∞, G$\underline{\infty}$; Hemlock, K5, C5, A5, G$\underline{(2)}$; *Artemisia*, K0, C(5), A(5), G$\underline{(2)}$.

By displacement of the floral members, by inequalities in their size, or by the suppression of some of them, the original radial (actinomorphic) construction (Fig. 525 *A*) is modified (cf. p. 72); either dorsiventral (zygomorphic) flowers (Fig. 525 *B*) or completely asymmetrical flowers (Fig. 525 *C*) may result. In the floral formula $\oplus$ indicates an actinomorphic and $\downarrow$ a zygomorphic flower, *e.g.* Laburnum, $\downarrow$ K5, C5, A (5 + 5), G1. Zygomorphic flowers always tend to assume a definite position in relation to the vertical. Radial monstrosities of normally dorsiventral flowers are termed peloric.

2. Ecology. Pollination of Flowers (4) (cf. p. 201).—Many differences in the structure of flowers and in the arrangement of their organs which would otherwise be doubtful are explained when brought into relation to the functions performed by the flower. All flowers have the function of producing progeny sexually; the

methods leading to this common end are, however, very various. In contrast to the Bryophyta and Pteridophyta in which the union of the sexual cells is effected by the aid of water, the Spermatophyta, which do not separate a motile male gamete, and have the egg-cells permanently enclosed in the tissues of the parent plant, are forced to adopt other methods. Arrangements to convey the microspores, enclosing the male sexual cell, to the macrospores, enclosed in the macrosporangia and containing the egg-cells, become necessary.

A large number of Spermatophyta make use of the wind to convey the microspores, *i.e.* the pollen, to its destination. Examples are all the Conifers, and also the majority of our native deciduous trees such as the Elm, Oak, Beech, Hornbeam, and further our Grasses and cereals. Simple as the relations in this case appear to be, various

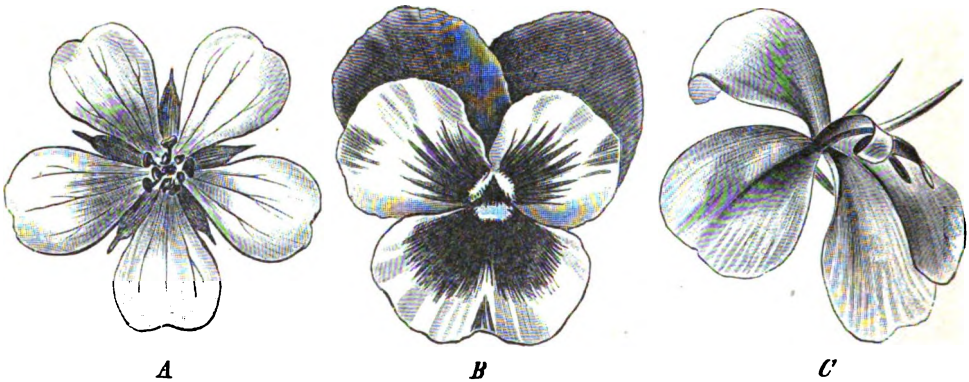


FIG. 525.—*A*, Actinomorphic flower of *Geranium sanguineum*. *B*, Zygomorphic flower of *Viola tricolor*. *C*, Asymmetrical flower of *Canna indica*.

necessary preliminaries are required for successfully effecting this method of pollination.

It is especially necessary that such ANEMOPHILOUS plants should produce a very large quantity of pollen, since naturally only a small fraction of what is shed will reach its destination. Thus at the season when our coniferous woods are in flower large quantities of pollen fall to the ground, constituting what is known as sulphur showers.

Anemophilous plants exhibit some characters in common which stand in definite relation to wind-pollination. The male inflorescence has usually the form of a longer or shorter catkin (Fig. 526) which bears a large number of microsporophylls; these are so oriented that after the sporangia have opened the pollen can be readily carried away by the wind. Examples are the catkins of the Oak (Fig. 610), Birch (Fig. 604), Alder, Hazel, Hornbeam, and Walnut; the catkins of the last-named plant (Fig. 602) are especially long. The male flowers of the Coniferae (Fig 510) are similar. The mode of attachment of the

anthers of Gramineae on long slender filaments has the same significance. The pollen grains of anemophilous flowers also have characteristic features. They are light and smooth, and in some Conifers are even provided with two wing-like sacs (Fig. 510 *D*), which enable them to remain suspended longer in the air. Some Urticaceae (*Pilea*, *Urtica*) scatter the pollen on the opening of the elastically-stretched wall of the pollen sac as a light cloud of dust.

The female flowers are usually not brightly coloured and do not develop nectaries. The stigmas, which catch the pollen, are strongly developed and provided with long feathery hairs (Fig. 527), or their form is brush-like, pinnate or elongated, and filamentous. In many Gymnosperms (*e.g. Taxus*) the macrosporangium excretes a drop of fluid in which the pollen grains are caught; on drying up of the drop the pollen is drawn down on to the tip of the nucellus. In other cases the pollen grains glide down between the carpellary scales of the cones till they reach the moist micropyles of the ovules and adhere to them.

FIG. 526. — Catkin of *Corylus americana*. (After DUCHARTRE.)

Lastly, the time of flowering is not without importance. The Elm flowers in February and March long before its leaves develop, and the same holds for the Hazel, Poplar, and Alder. In the Walnut, Oak, Beech, and Birch the flowers open when the first leaves are unfolding, and flowering is over before the foliage is fully expanded. Were this not so, much of the pollen would be intercepted by the foliage leaves, and even more pollen would need to be produced than has to be done to ensure fertilisation. In the Conifers the foliage presents less difficulty, but here the female cones are borne at the summit of the tree (*Abies*) or high up (*Picea*), while the male flowers are developed on lower branches. The pollen grains are shed in warm dry weather, and carried up in the sunshine by ascending currents of air till they reach their destination on the female cones situated high above the male flowers.

Only a small number of Phanerogams make use of the agency of water for effecting their pollination, and are, on that account, termed HYDROPHILOUS PLANTS. This applies only to submerged water plants which do not emerge from the medium, *e.g. Zostera*, Seawrack.

The great majority of Phanerogams are dependent upon animals, especially on insects, for the transference of their pollen. Plants pollinated by the aid of insects are termed ENTOMOPHILOUS.

Since KONRAD SPRENGEL in his famous work, *Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen*, 1793, revealed the mutual relations between the forms and colours of flowers

and the insects that frequent them, no other department of biology has been more actively studied than floral ecology. It is the more remarkable that no one had put the question whether the colours seen by our eyes were also perceived by the insects in the same way. It was difficult to think of the display of colour in meadow or orchard otherwise than as an apparatus of attraction for the visiting insects seeking the food provided by the nectaries of the flowers. We owe the opening up of this question to C. HESS (5). In the light of his exact demonstration that bees are colour-blind the earlier views require to be revised.

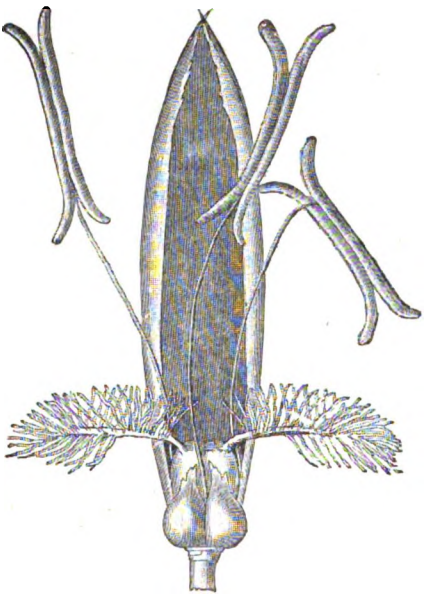


FIG. 527.—Anemophilous flower of *Festuca elatior*. (After SCHENCK.)

HESS bases his argument on the comparison of the behaviour of bees with colour-blind human beings, and shows that they, like all invertebrate animals that have been investigated, react quite similarly to the stimuli of colour. Their brightness-maximum lies in the green-yellow region; red appears dark, and blue on the other hand light. The attraction of flowers for bees must accordingly depend on the contrast effects of different degrees of brightness.

In this demonstration there appears to be wanting the answer to the question at what distances the eyes of the bee are able to perceive strong contrasts in brightness. An orchard in flower, apart from any colour-sense on the part of bees, would be more readily seen by them at a distance on account of the bright flowers contrasting with the dark background of foliage. To this would be added the tendency of bees, at least of the same colony, to collect together, so that when one bee has found a source of food, a crowd of others will follow.

The facts regarding the pollination of flowers by insects which SPRENGEL discovered still hold, although the particular question as to how the apparatus rendering the flowers conspicuous affects the eyes of insects, and how the conspicuousness has come about, is open to reconsideration. It must be borne in mind that without any relation to insect-pollination the Firs, Larch, and other Coniferae exhibit intensely-coloured female cones, as do the male flowers of the Pine when seen in mass. It would appear to be frequently of importance to plants for their reproductive organs to have some colour other than green. The greater absorption of heat-rays may be con-

nected with the red stigmas of the early-flowering Hazel, and perhaps also in the case of the cones of Coniferae. Deeper investigation may perhaps disclose further connections of this nature.

The relation between flowers and insects depending on the sense of form and scent of the latter remains unquestioned, and has been more fully investigated for bees by V. FRISCH. What explanation of the strong scent, increasing towards evening, of *Lonicera*, *Philadelphus*, etc., can be given except that it serves as an attraction to night-flying insects, such as Hawk-moths, which are led by the scent to find their food? How could the existence of nectaries and the excretion by the plant of an important reserve food substance be accounted for, if the guests which greedily consume it were not indispensable to the flowers? How, lastly, could the construction of a dorsiventral flower, such as that of *Salvia* or of *Orchis*, be understood if we did not relate it to the insects which visit the flower in search of nectar, and in doing so effect pollination? The mutual adaptations between the form of flowers and the bodies of insects are so numerous, and the experimental fact that plants removed from their native country, though growing healthily, remain sterile owing to the lack of the pollinating insects to which they are adapted, is so well established, that no doubt can be entertained on the mutual adaptations of flowers and insects. Usually the position of the nectaries is such that the hairy body of the visiting insect must carry away pollen from the flower; often the pollen will be deposited on special regions of the insect's body and, when another flower is visited, will be deposited on the stigma. It is of importance that the pollen of such entomophilous plants differs from that of the anemophilous flowers described above. Pollen grains provided with spiny projections, or with a rough or sticky surface, are characteristic of entomophilous plants; the grains may remain united in tetrads or in larger masses representing the contents of a whole pollen-sac (*Orchis*, *Asclepias*). The pollen itself forms a valuable nitrogenous food for some insects such as bees; these form "bee-bread" from it.

An example of a very close relation between floral construction and the body of the visiting insect is afforded by the pollination of *Salvia pratensis* by Humble Bees. Fig. 528, 1, shows a flower of *Salvia* with a Humble Bee on the lower lip in search of nectar. The flower has only two stamens, the two halves of each anther being quite differently developed, and separated by an elongated connective; the one half-anther is sterile and forms a projection in the throat of the corolla-tube, the other at the end of the long arm of the connective is fertile and lies beneath the hood formed by the upper lip of the corolla. The connective thus forms a lever, with unequal arms, movable on the summit of the short filament. When the bee introduces its proboscis it presses on the short arm of the lever; the fertile half-anther is thus by the movement of the connective (*c*) on its place of attachment to the filament (*f*) brought down against the hairy dorsal

surface of the insect's body (Fig. 528, 1, 3). On visiting an older flower the insect will meet with the stigma projecting further from the upper lip on the elongated style (Fig. 528, 2). The stigma is then in the position corresponding to the depressed half-anthers, and will receive with certainty the pollen deposited from them on the back of the bee.

In addition to the stimulus of hunger, plants utilise the reproductive instinct of insects for securing their pollination. Not a few plants (*Stapelia*, *Aristolochia*, and members of the Araceae), by the unnatural colour of their flowers combined with a strong carrion-like stench, induce carrion-flies to visit them and deposit their eggs; in so doing they effect, at the same time, the pollination of the flowers. In the well-known hollow, pear-shaped inflorescences of the Fig (*Ficus carica*, Fig. 614) there occur, in addition to long-styled female flowers that produce seeds, similar gall-flowers with short styles. In each of the latter a single egg is laid by the Gall-wasp (*Blastophaga*), which, while doing this, pollinates the fertile flowers with pollen carried from the male inflorescence (the Caprificus). The large white

FIG. 528.—Pollination of *Salvia pratensis*. Explanation in the text. (After F. NOLL.)

flowers of *Yucca* are exclusively pollinated by the Yucca moth (*Pronuba*). The moth escapes from the pupa in the soil at the time of flowering of *Yucca* and introduces its eggs into the ovary by way of the style; in doing this it carries pollen to the stigma. The larvae of the moth consume a proportion of the ovules in the ovary, but without the agency of the moth no seeds will be developed, as is shown by the sterility of the plant in cultivation.

ORNITHOPHILY plays a much less important part than entomophily; the bird-visitors are confined to the American Humming-birds and the Honey Birds of the Old World. A specially remarkable case of adaptation of this kind is afforded by *Strelitzia reginae*, which is often cultivated in greenhouses (Fig. 529). Its three outer perianth segments (*t*) are of a bright orange colour; the large azure-blue labellum (*p*) corresponds to one of the inner perianth leaves, while the other two (*p*) remain inconspicuous and roof over the passage leading to the nectary. The stamens (*st*) and the style (*g*) lie in a groove, the margins of which readily separate, formed by the labellum, while the stigma (*q*) projects freely. The similarly-coloured and showy bird (*Nectarinia afra*) flies first to the stigma and touches it, then secures pollen from the stamens, which it will deposit on the stigma of the flower next visited.

The structure of the pendulous inflorescence of *Marcgravia* is just as remarkable (Fig. 530); in this the bracts form receptacles containing the nectar. Numerous insects fly around these nectaries, and the darting Humming-birds, either in pursuit

of the insects or themselves in search of nectar, get dusted with pollen from the flowers, which face downwards, and carry it to other flowers. On the investiga-

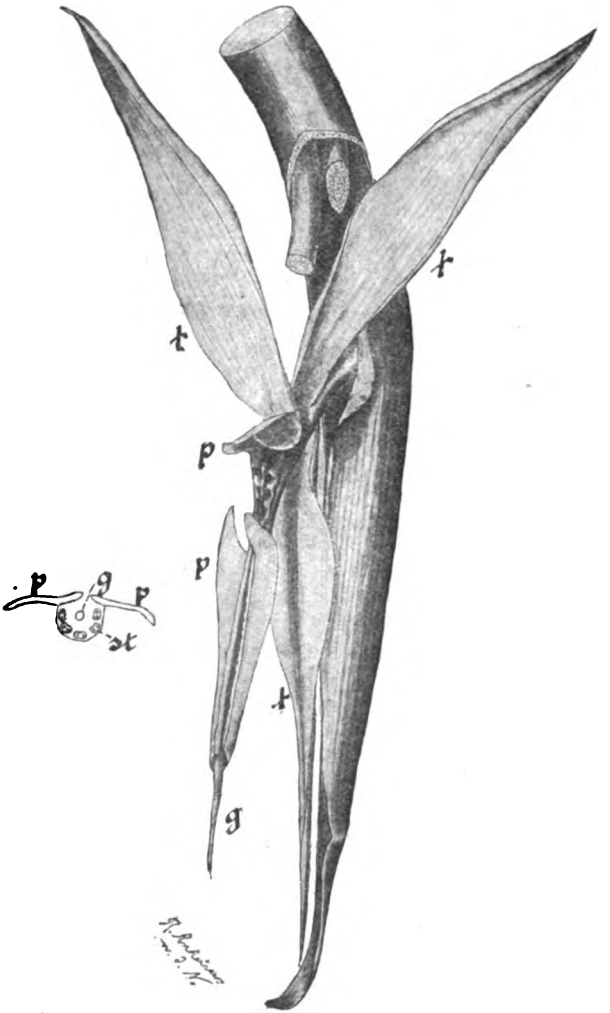


FIG. 529.—Ornithophilous flower of *Strelitzia reginae* and a cross-section of its large labellum (*p*); *t* outer, and *p* inner perianth leaves; *g*, style and stigma; *st*, stamens. (From SCHIMPER, *Plant Geography*.)

tions of HESS referred to above, it is easy to understand why the majority of ornithophilous flowers (*Aloë*, *Clianthus*, epiphytic Loranthaceae, etc.) are red, since this colour has the same value to the eyes of day-flying birds as to our own.

Besides these ORNITHOPHILOUS plants there are a few visited by Bats

(CHIROPTEROPHILOUS); thus the dicecious Pandanaceous plant *Freycinetia* of the Malayan Archipelago is pollinated by a Flying Fox (*Pteropus*), which eats the inner bracts.

Pollination in some cases is effected by means of snails (MALACOPHILOUS PLANTS). To their instrumentality the flowers of *Calla palustris*, *Chrysosplenium*, and also the half-buried flowers of the well-known *Aspidistra* owe their pollination.

It would seem remarkable that such manifold and various adaptations for the conveyance of pollen should exist while the majority of

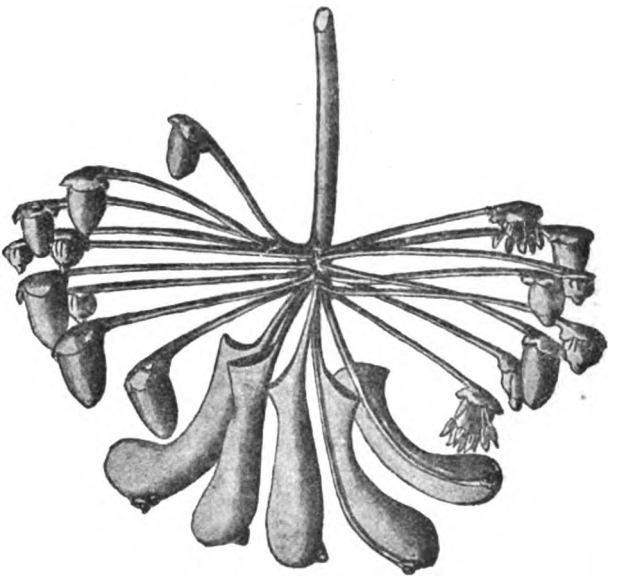


FIG. 530.—Inflorescence of *Marcgravia umbellata* adapted for pollination by Humming-birds. (From SCHIMPER, *Plant Geography*.)

angiospermic plants have hermaphrodite flowers; it is known, however, that the pollination of a flower with its own pollen may result in a poorer yield of seed (Rye) or be without result (self-sterility in *Cardamine pratensis*, *Lobelia fulgens*, *Corydalis cava*, etc.).

Cross-pollination (allogamy) must take place when the pollen can only germinate if the stigma is rubbed as in the case of *Laburnum vulgare*. The insect visit, which as a rule will bring foreign pollen, prepares the conditions for germination and excludes the action of the flower's own pollen. In the Orchids the flower's own pollen has a directly injurious influence, and when applied to the stigma causes the flower to wither.

Even when there is no self-sterility there are many and various conditions which render the self-fertilisation of hermaphrodite flowers

impossible and favour cross-pollination. It is obvious that dioecism completely prevents self-fertilisation, and that monoecism at least

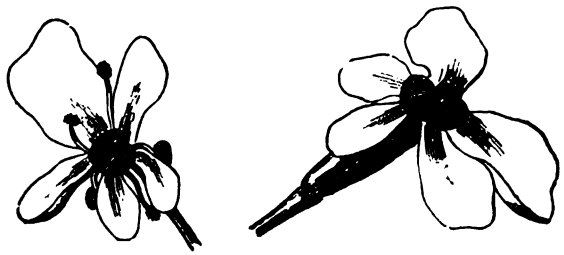


FIG. 531.—Flower of *Anthriscus sylvestris*. Slightly magnified. *1*, In the male, *2*, in the female condition. (After H. MÜLLER.)

hinders the pollination of the flowers with pollen from the same plant. A similar result is brought about when the two kinds of sexual organs of a hermaphrodite flower mature at different times. This very frequent condition is known as DICHOGAMY. There are obviously two possible cases of dichogamy. Either the stamens mature first and the pollen is shed before the stigmas of the same flower are receptive; the plant is known as PROTANDROUS. On the other hand, the style with its stigma may ripen first, before the pollen is ready to be shed; the plant is PROTOGYNOUS.

PROTANDRY is the more frequent form of dichogamy. It occurs in the flowers of the Geraniaceae, Campanulaceae, Compositae, Lobeliaceae, Umbelliferae (Fig. 531), Geraniaceae, Malvaceae (Fig. 664), etc. The anthers, in this case, open and discharge their pollen at a time when the stigmas of the same flowers are still imperfectly developed and not ready for pollination. In *Salvia* also (Fig. 525) protandry is the necessary preliminary to the cross-pollination.

FIG. 532.—Inflorescence of *Plantago media* with protogynous flowers. The upper, still closed flowers (♀) have protruding styles; the lower (♂) have lost their styles, and disclose their elongated stamens. (After F. NOLL.)

In the less frequent PROTOGYNY the female sexual organs are ready for fertilisation before the pollen of the same flowers is ripe, and the stigma is usually pollinated and withered before the pollen is shed (*Scrophularia nodosa*, *Aristolochia clematitis*, *Helleborus*, *Magnolia*, *Plantago*, Fig. 532).

The effect of HETEROSTYLY discovered by DARWIN is similar. According to TISCHLER this condition can be altered by the conditions of nutrition. A good example is afforded by *Primula sinensis* (Fig. 533). Comparison of the flowers on different individuals shows that they differ as regards the position of the stamens and stigma. There are long-styled flowers, the stigma standing at the entrance to the corolla-tube, while the anthers are placed deep down in the tube; and short-styled flowers, the stigma of which stands at the height of the anthers, and the stamens at the height of the stigma of the long-styled flower. An insect will naturally only touch organs of corresponding height with the same part of its body and thus carry pollen between the male and female organs of corresponding height. Thus cross-pollination is ensured. The relative sizes of the pollen grains and stigmatic papillae agree with this cross-pollination.

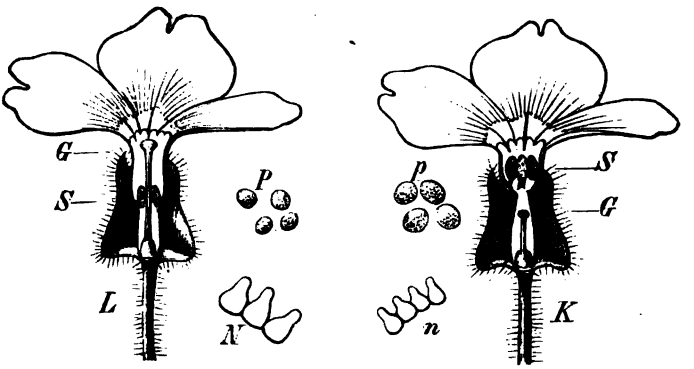


FIG. 533.—*Primula sinensis*: two heterostyled flowers from different plants. *L*, Long-styled, *K*, short-styled flowers; *G*, style; *S*, anthers; *P*, pollen-grains, and *N*, stigmatic papillae of the long-styled form; *p* and *n*, pollen-grains and stigmatic papillae of the short-styled form. (*P*, *N*, *p*, *n*, × 110. After NOLL.)

The same DIMORPHIC HETEROSTYLY is exhibited by *Pulmonaria*, *Hottonia*, *Fagopyrum*, *Linum*, and *Menyanthes*. There are also flowers with TRIMORPHIC HETEROSTYLY (*Lythrum salicaria*, and some species of *Oxalis*) in which there are two circles of stamens and three variations in the height of the stigmas and anthers.

In a great number of flowers self-pollination is made mechanically impossible, as their own pollen is prevented by the respective positions of the sexual organs from coming in contact with the stigma (HERCOGAMY). In the Iris, for example, the anthers are sheltered under the branched petaloid style. The pollinia of *Orchis* are retained in position above the stigma; in *Asclepias* the five pollinia are attached in pairs to swellings of the style by adhesive discs (cf. Fig. 746).

Sometimes hercogamy and dichogamy occur together. The flowers of *Aristolochia clematitis* (Fig. 534) are protogynous. The conveyance of pollen

from the older to the younger flowers is effected by small insects. The flowers at first stand upright with a widely-opened mouth (Fig. 534 *I*), and in this condition the insects can easily push past the downwardly-directed hairs which clothe the tubular portion of the corolla and reach the dilated portion below. Their exit is, however, prevented by the hairs until the stigma has withered and the anthers have shed their pollen. When this has taken place (Fig. 534 *II*) the hairs dry up, and the insects covered with pollen can make their way out and convey the pollen to the receptive stigmas of younger flowers.

All these varied and often highly specialised arrangements to ensure crossing indicate a tendency to favour the union of sexual cells which differ in their hereditary characters more widely from one another than would be the case if derived from the same flower. The progeny from allogamous fertilisation tend to be stronger than from autogamous fertilisation.

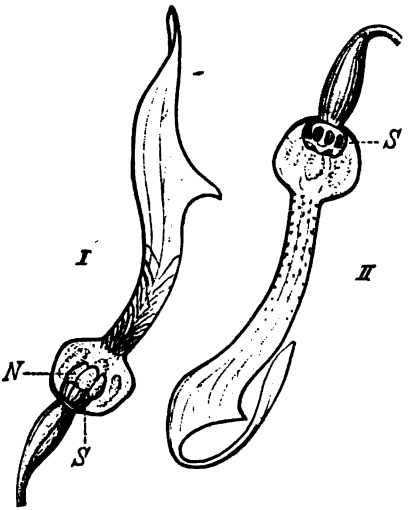


FIG. 534. — Flowers of *Aristolochia clematitis* cut through longitudinally. *I*, Young flower in which the stigma (*N*) is receptive and the stamens (*S*) have not yet opened. *II*, Older flower with the stamens opened, the stigma withered, and the hairs on the corolla dried up. (× 2. After F. NOLL.)

In certain plants in addition to the large CHASMOGAMOUS flowers, pollinated by wind or insects, small inconspicuous flowers occur which never open and only serve for self-fertilisation; these CLEISTOGAMOUS flowers (6) afford a further means of propagating the plant, while the plants have the opportunity of occasional cross-pollination owing to the presence of the large chasmogamous flowers. Cleistogamy is of frequent or regular occurrence in species of *Impatiens*, *Viola*, *Lamium*, and *Stellaria*, in *Specularia perfoliata*, *Juncus bufonius*, etc. *Polycarpon tetraphyllum* has only cleistogamous flowers.

Development of the Sexual Generation in the Phanerogams

A. In the **Gymnosperms** (7) a prothallium consisting of a few cells is formed on the germination of the MICROSPORE. This lies within the large cell, which will later give rise to the pollen-tube, closely applied to the cell wall; the nucleus of this cell is marked *k* in Fig. 536 *A*. The first-formed cell (*p*) corresponds to the vegetative cells of the prothallium. The SPERMATOGENOUS CELL (*sp*), which is cut off last, divides later into the MOTHER CELL OF THE ANTHERIDIUM (Fig. 536 *B*, *m*), and a STERILE SISTER CELL (*s*) adjoining the prothallial cell. It is by the breaking down or the separation of the sterile sister cell that the antheridial mother cell becomes free to pass into the pollen-tube. There, or before its separation, it divides into two daughter cells; these are the GENERATIVE CELLS or MALE SEXUAL CELLS.

(a) Cycadeae

In the Cycadeae and in *Ginkgo* these male cells still have the form of spermatozoids, and thus connect directly with the heterosporous Archegoniatae. Their mode of development is shown for *Zamia* in Fig. 536. The description of the figure deals with the details. As is further shown in Fig. 537 (*a*) the two spermatozoids remain for a time back to back attached to the sister cell of the antheridium; after their separation (*b*) they round off, the anterior end being provided with a spirally-arranged crown of cilia by means of which they are capable of independent movement (Fig. 538).

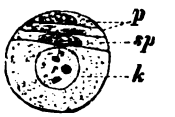


FIG. 535.—Pollen-grain of *Ginkgo biloba* still within the microsporangium. (× 300. After STRASBURGER.)

The female cones of *Zamia* bear numerous sporophylls, the hexagonal shield-shaped terminal expansions (Fig. 583) of which fit closely together. Each sporophyll bears a pair of macro-

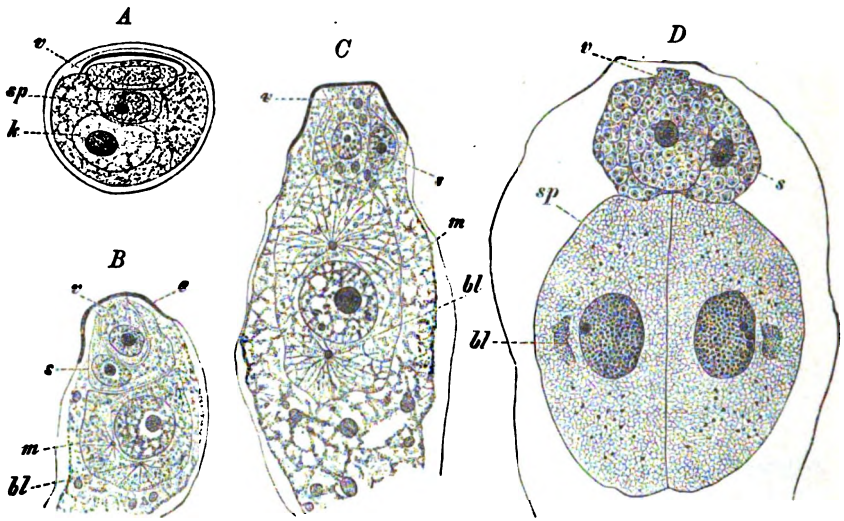


FIG. 536.—Formation of spermatozoids in *Zamia floridana*. *A*, Mature pollen-grain (× 800); *v*, vegetative prothallial cell—the dark streak at its base indicates the position of another crushed cell; *k*, nucleus of the pollen-tube; *sp*, spermatogenous cell. *B*, *C*, *D*, Stages in the development of the antheridium (*B*, *C* × 400; *D* × 200); *v*, persisting vegetative cell growing into the sterile sister cell of the antheridium (*s*); *m*, mother cell of the antheridium, *i.e.* mother cell of the spermatozoids; *e*, exine. In the mother cell the large blepharoplasts (*bl*) which form the cilia are visible; in *B* and *C* they are star-shaped, while in *D* they are composed of small granules, which will form the cilium-forming spiral band. Starch-grains are present in the pollen-tube, and in *C* they are appearing in the vegetative cell and the sister cell, both of which in *D* are packed with starch. In *D* the two spermatozoids (*sp*) derived from the mother cell are seen divided from one another by a wall. (After H. J. WEBBER.)

sporangia. The macrosporangium consists of the nucellus and an integument. The micropyle forms an open canal above the tip of

the nucellus. At the period during which the male cones are shedding their pollen, the macrosporophylls become slightly separated from one another so that the wind-borne pollen-grains can readily enter. A more or less extensive cavity (POLLEN-CHAMBER, Fig. 539) has by this time been formed at the apex of the nucellus, while the disintegrated cells, together perhaps with fluid excreted from the surrounding cells of the nucellus, have given rise to a sticky mass which fills the micropylar canal and forms a drop at its entrance. The pollen-grains reach this drop and, with the gradual drying up of the fluid, are drawn through the micropylar canal into the pollen-chamber.

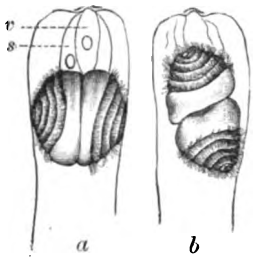


FIG. 537.—Upper end of the pollen-tube of *Zamia floridana*, showing the vegetative prothallial cell (*v*), the sterile sister cell (*s*), and the two spermatozoids. *a*, Before movement of the spermatozoids has commenced; *b*, after the beginning of ciliary motion; the prothallial cell is broken down and the separation of the two spermatozoids is taking place. (× circa 75. After H. J. WEBBER.)

During the development of the pollen-tube (Fig. 510) and the formation of the motile spermatozoids, the embryo-sac filled with the prothallial tissue is increasing in size within the nucellus. As in the Coniferae the embryo-sac arises by the tetrad division of an embryo-sac mother cell which usually

FIG. 538.—*Zamia floridana*. Mature, free-swimming spermatozoid. (× 150. After H. J. WEBBER.)

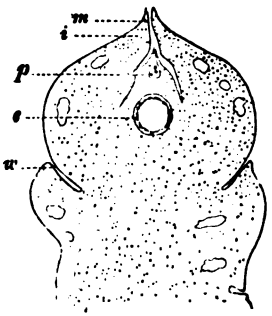


FIG. 539.—Longitudinal section of a young macrosporangium of *Ginkgo biloba*. *m*, Micropyle; *i*, integument; *p*, pollen-chamber; *e*, embryo-sac; *w*, outgrowth of sporophyll. (× 35. After COULTER and CHAMBERLAIN.)

crushes the other sporogenous cells, as in the case of the macrosporangium of *Selaginella*. As it crushes the tissue of the upper portion of the nucellus it approaches the base of the pollen-chamber.

At the apex of the embryo-sac are found the archegonia, usually four in number, and separated from one another by some layers of cells.

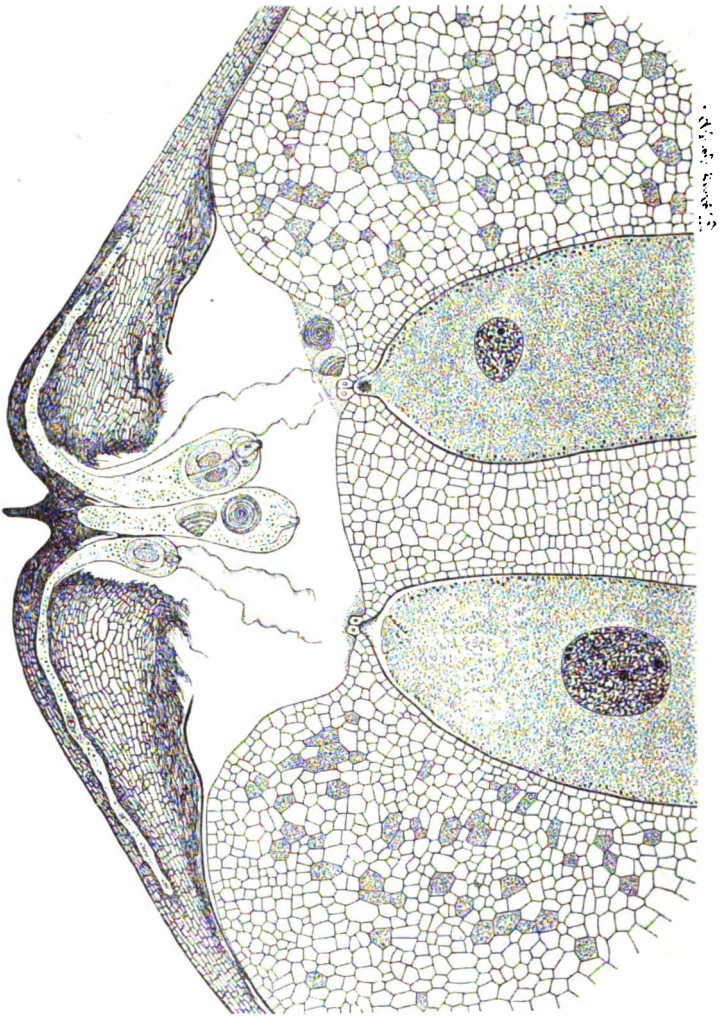


FIG. 540.—*Dioon edule*. Upper portion of the nucellus at the period of fertilisation. The pollen-tubes have grown down from the pollen-chamber through the nucellus after becoming attached by lateral outgrowths. They have reached the archegonial chamber and two of them have already liberated their contents. Two large archegonia with projecting neck-cells are present. (After CHAMBERLAIN.)

Each archegonium has a neck, and ultimately cuts off a canal-cell. The archegonia are situated at the base of a depression in the pro-

thallium, the archegonial chamber (Fig. 540), which in *Dioon* is about 1 mm. in depth and 2 mm. across. The pollen-tubes grow into this depression and liberate their spermatozoids together with a drop of watery fluid in which they swim. The spermatozoids require to narrow considerably in order to pass through the space between the neck-cells. The spermatozoid strips off the ciliated band on entering the protoplasm of the egg, and its nucleus fuses with that of the latter. The nucleus of the fertilised ovum (Fig. 541) soon divides, and the daughter nuclei continue to divide rapidly, until after the eighth division there are about 256 free nuclei within the cell. These

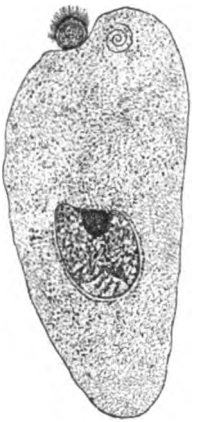


FIG. 541.—*Zamia floridana*. An ovum immediately after the fusion of the nucleus of a spermatozoid with the female nucleus has taken place. The ciliary band of the spermatozoid remains in the upper portion of the protoplasm of the ovum. A second spermatozoid has attempted to enter the ovum. (× 18. After H. J. WEBBER.)

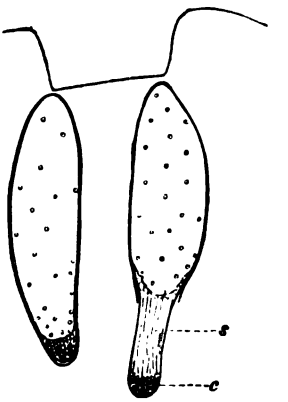


FIG. 542.—Two young pro-embryos of *Dioon edule* showing their relation to the archegonial chamber. *S*, suspensor; *e*, embryo. (After CHAMBERLAIN.)

are crowded towards the lower end of the fertilised egg, where cell walls commence to form between them.

The so-called PRO-EMBRYO is thus formed (Fig. 542), at the growing end of which the embryo develops from relatively few cells. The cells farther back elongate greatly and as a SUSPENSOR carry the embryo into the prothallus. This in Spermatophytes is termed the ENDOSPERM and serves as a nutritive tissue for the growing embryo. The latter ultimately develops, at the end directed into the prothallus, two large COTYLEDONS between which is the rudiment of the apical bud or PLUMULE. The region of the stem below the cotyledons is termed the HYPOCOTYL; it passes gradually into the main root or RADICLE, which is always directed towards the micropyle.

(b) Coniferae

The development of the microspores of the Coniferae when they germinate differs from the process described above. The prothallial

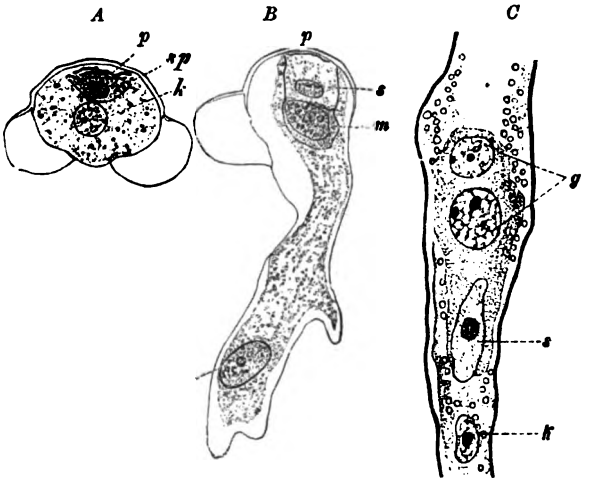


FIG. 543. — Development of the pollen-tube. *A*, *B*, *Pinus laricio* (× 300. After COULTER and CHAMBERLAIN). *C*, *Picea excelsa* (× 250. After MIYAKE). *p*, Remains of the prothallial cells; *sp*, spermatogenous cell; *m*, antheridium mother cell; *s*, its sterile sister cell; *g*, generative nuclei of unequal size in a common protoplasmic body; *k*, pollen-tube nucleus.

cells, the number of which in the ancient genus *Araucaria* is larger than in the other Coniferae and the Cycadeae, soon collapse (Fig. 543 *A*, *B*), and the generative cells never have the form of spermatozoids. The gap between the Coniferae and the Pteridophyta is thus a wider one.

The Abietineae have two generative nuclei of unequal size in the one protoplasmic body; only the larger nucleus which goes first is fertile (Fig. 543 *C*, *g*).

FIG. 544.—*Taxus baccata*. Longitudinal section through the sporogenous tissue, showing an embryo-sac mother cell which has undergone the tetrad division; three of the facultative macrospores are degenerating, while the fourth is undergoing further development. (× 250. After STRASBURGER.)

In *Araucaria* the prothallial tissue is highly developed. The spermatogenous cell gives rise to the sterile cell and the antheridium mother cell. From the latter two generative nuclei, which to begin with are of equal size, are produced; they are enclosed in a common protoplasmic mass. In many cases one of the two nuclei appears to gradually diminish in size.

Araucaria thus stands nearest to the Abietineae. In the Cupressineae two equal generative cells are found throughout. *Taxus* has a single generative cell; the sister cell produced on the division of the antheridium mother cell is greatly reduced.

As a rule the macrosporophylls bear two macrosporangia. The single mother cell undergoes a tetrad division (Fig. 544), and of the four resulting cells only one develops into an embryo-sac (macrospore). This, as it increases in size, first crushes its sister cells and later the whole sporogenous complex of cells. Meanwhile, by the repeated division of the nucleus and protoplasm, the macrospore becomes filled with the

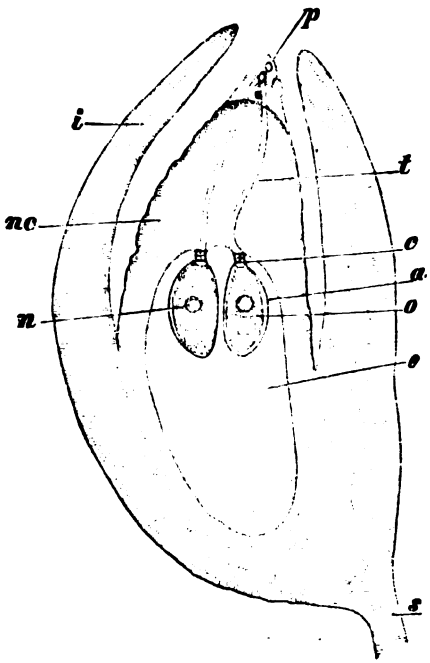


FIG. 545.—Median longitudinal section of an ovule of *Picea excelsa* at the period of fertilisation. *e*, Embryo-sac filled with the prothallium; *a*, archegonium showing ventral (*a*) and neck portion (*c*); *o*, egg-cell; *n*, nucleus of egg-cell; *nc*, nucellus; *p*, pollen-grains; *t*, pollen-tube; *i*, integument; *s*, seed-wing. (× 9. After STRASBURGER.)

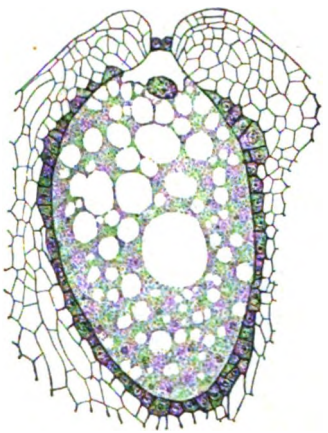


FIG. 546.—Archegonium of *Pinus laricio* before the separation of the ventral-canal-cell. (× 104. After COULTER and CHAMBERLAIN.)

tissue of the prothallium (Fig. 545). The archegonia are formed at the apex of the prothallium; each consists of a large ovum and a short neck. As in the Pteridophytes a small ventral canal-cell is cut off from the egg-cell shortly before fertilisation (Fig. 546). The development of the embryo from the fertilised ovum presents great differences in the several orders and even genera, and the following description applies to the species of *Pinus* (Fig. 547 *D-K*).

By two successive divisions of the nucleus four nuclei are formed which pass to the base of the egg-cell, where they arrange themselves

in one plane and undergo a further division. Cell walls are formed between the eight nuclei of this eight-celled pro-embryo. The cells form two tiers, those of the upper tier being in open communication with the cavity of the ovum. The four upper cells then undergo another division (*G*), and this is followed by a similar division of the four lower cells (*H*). The PRO-EMBRYO thus consists of four tiers, each containing four cells, the cells of the upper tier being continuous with

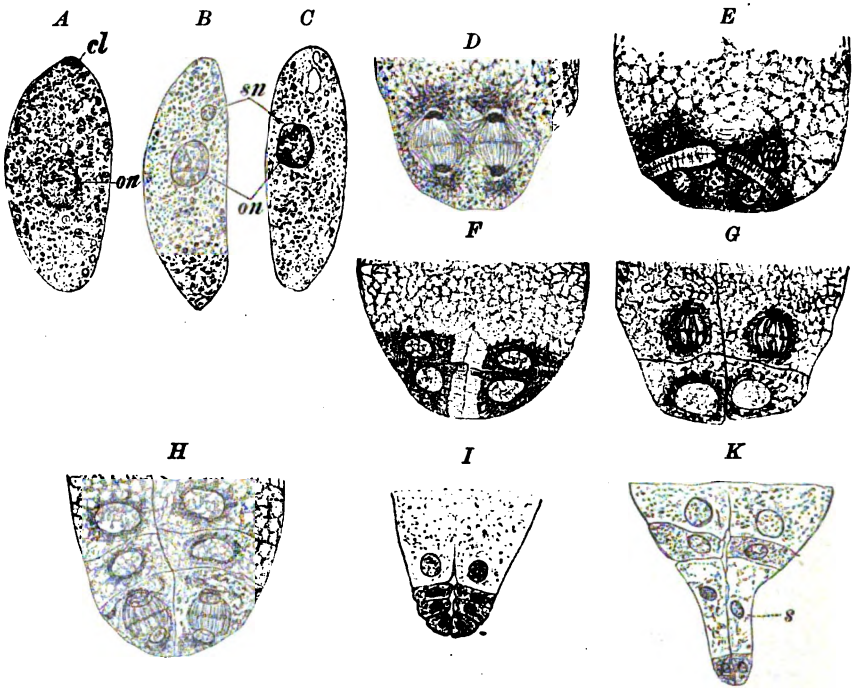


FIG. 547.—*Picea excelsa* (*A-C*). *Pinus laricio* (*D-K*). *A*, Mature ovum with its nucleus (*on*) and the ventral-canal-cell (*cl*). *B*, The male nucleus (*sn*) within the ovum. *C*, Fusion of the male and female nuclei. *D-K*, Description in text; *s*, suspensor. (*A-C* × 55, after MIYAKE; *D-H* × 200, after KILDAHL; *I*, *K* × 104, after COULTER and CHAMBERLAIN.)

the remaining portion of the ovum. In the further development of the three lower tiers the middle tier elongates to form the SUSPENSOR (*K*, *s*), pushing the terminal tier from which the embryo will arise into the tissue of the prothallium or endosperm; the cells of the latter are filled with nutritive reserve material.

In other genera a separation of the four rows of cells takes place, and each bears a young embryo. As a rule, however, only a single embryo continues its development in each macrospore, although several archegonia may have been fertilised. The embryo is formed of the

same parts as the embryo in the Cycadeae, but the number of cotyledons is frequently greater than two.

(c) Gnetineae

The last order of Gymnosperms, the Gnetineae, exhibit a peculiar and isolated course of development. The microspores in their development and

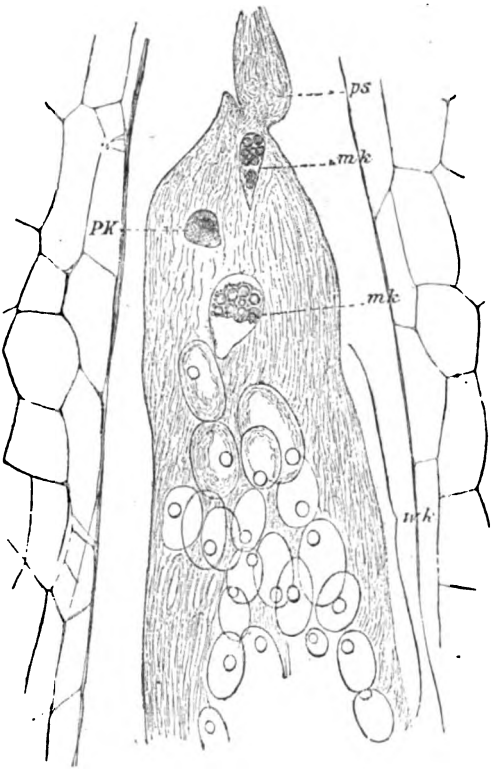


FIG. 548.—Apex of the embryo-sac of *Gnetum Rumphianum* shortly before the development of the female cells. *wk*, Female nuclei; *mk*, male nuclei; *PK*, pollen-tube nucleus; *ps*, pollen-tube. (× 500.)

germination show no essential differences from those of other Gymnosperms; the separation of the generative cells is, however, less clear and sometimes wanting in that two similar nuclei lie in the common protoplasmic investment. The macrospores show more marked peculiarities. The macrospores of *Ephedra* and *Welwitschia* have well-developed prothallia. *Ephedra* forms archegonia which on the whole resemble those of the Coniferae. *Welwitschia* has elongated cells with 2-5 nuclei which grow from the summit of the prothallus into the tissue of the nucellus towards the entering pollen-tubes. Their significance as archegonia is not clear. In *Gnetum* (Fig. 548) no prothallium is formed, but the embryo-sac

becomes filled with protoplasm in which are numerous nuclei. Each of the two generative cells from the pollen-tube fuses with a female nucleus. Of all the fertilised cells resulting from the penetration of a number of pollen-tubes to the embryo-sac only one develops into an embryo.

B. Angiosperms (8)

(*a*) The MICROSPORES of Angiosperms before they are shed from the pollen-sac form an antheridial mother cell (Fig. 549 *m*) which is

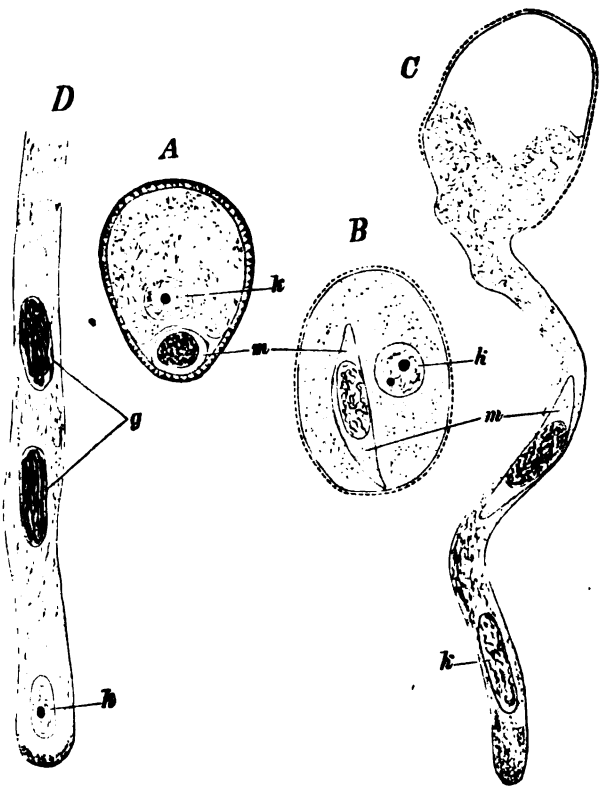


FIG. 549.—Pollen-grain of *Lilium Martagon* and its germination. *k*, Vegetative nucleus of the pollen-grain ; *m*, antheridial mother cell ; *g*, generative nuclei. (× 400. After STRASBURGER.)

clearly delimited from the large pollen-tube cell, but is not enclosed by a cell wall. When the pollen grain germinates on the stigma the antheridial cell passes into the pollen tube, and its nucleus sooner or later divides into two generative nuclei (*g*) which lie free in the protoplasm within the pollen-tube without being enclosed in a common mass of protoplasm. They are of an elongated oval or ellipsoidal

shape and pass one after another down the pollen-tube. The nucleus of the pollen-tube (*k*) is usually visible in the neighbourhood of the generative nuclei. The absence of the small prothallial cells, and of a sterile sister cell of the antheridium, as well as the absence of a cell wall from the mother cell of the antheridium, and lastly the presence of naked generative nuclei instead of generative cells in the pollen-tube, are points in which the Angiosperms differ from Gymnosperms.

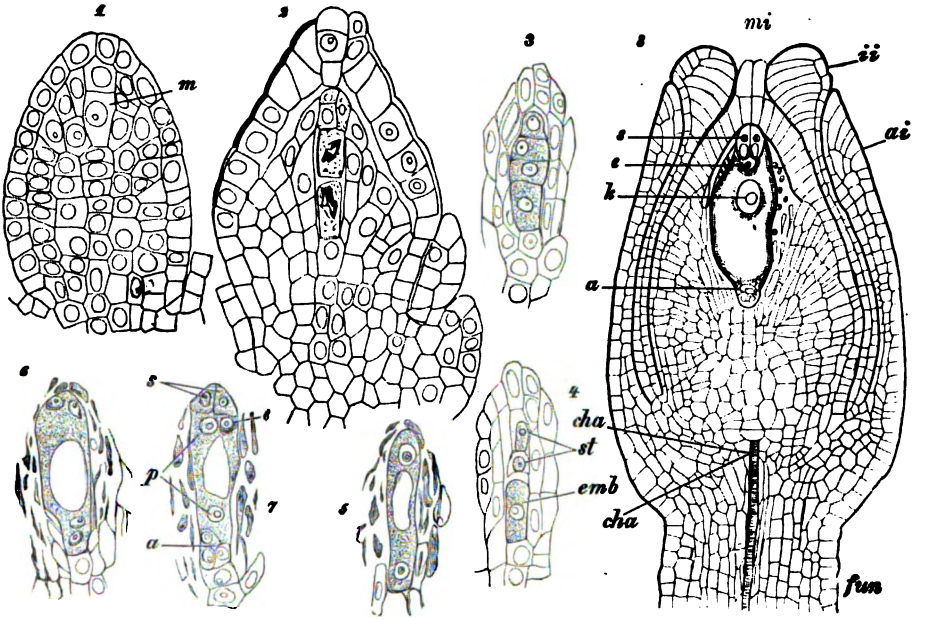


FIG. 550.—Development of the embryo-sac in *Polygonum divaricatum*. *m*, Mother cell of the embryo-sac; *emb*, embryo-sac; *st*, sterile sister cells; *e*, egg-cell; *s*, synergidae; *p*, polar nuclei; *a*, antipodal cells; *k*, secondary nucleus of the embryo-sac; *cha*, chalaza; *mi*, micropyle; *ai*, *ii*, outer and inner integuments; *fun*, funiculus. (*1-7* × 320, *8* × 135. After STRASBURGER.)

The reduction of the male prothallium has thus gone so far that only the indispensably necessary parts remain.

(*b*) MACROSPORES. — The characteristic differences which the Angiosperms show from the general course of development of the MACROSPORANGIUM in the Gymnosperms commence with the cell divisions in the single, functional, macrospore-mother-cell resulting from the tetrad division (Fig. 550, 1-5). The "PRIMARY NUCLEUS of the embryo-sac" divides and the daughter nuclei separate from one another. They divide twice in succession so that eight nuclei are present. After this, cell formation commences around these nuclei (Fig. 550, 6-8). Both at the upper or micropylar end of the embryo-

sac and at the lower end three naked cells are thus formed. The two remaining "POLAR NUCLEI" move towards one another in the middle of the embryo-sac, and fuse to form the "SECONDARY NUCLEUS of the embryo-sac." The three cells at the lower end are called the ANTIPODAL CELLS; they correspond to the vegetative prothallial cells, which in Gymnosperms and in *Gnetum* fill the cavity of the embryo-sac. The three cells at the micropylar end constitute the "EGG APPARATUS." Two of them are similar and are termed the SYNERGIDAE, while the third, which projects farther into the cavity, is the EGG-CELL or OVUM itself. The synergidae assist in the passage of the contents of the pollen-tube into the embryo-sac. Here also the process of reduction has gone as far as possible; in place of the more or less numerous archegonia of the gymnospermous macrospore only a single egg-cell is present.

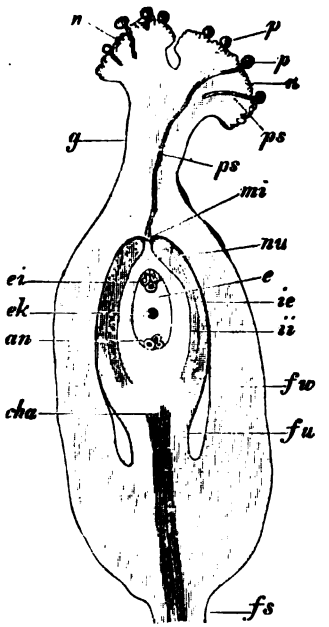


FIG. 551.—Ovary of *Polygonum Convolvulus* during fertilisation. *fs*, Stalk-like base of ovary; *fu*, funiculus; *cha*, chalaza; *nu*, nucellus; *mi*, micropyle; *ii*, inner, *ie*, outer integument; *e*, embryo-sac; *ek*, nucleus of embryo-sac; *ei*, egg apparatus; *an*, antipodal cells; *g*, style; *n*, stigma; *p*, pollen grains; *ps*, pollen-tubes. (× 48. After SCHENCK.)

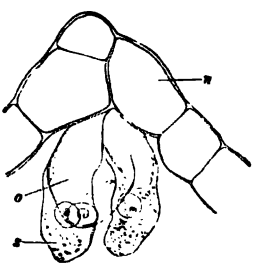


FIG. 552.—*Funkia ovata*. Apex of nucellus, showing part of embryo-sac and egg apparatus before fertilisation; o, egg-cell; s, synergidae. (× 390. After STRASBURGER.)

The significance of the synergidae is difficult to determine unless they are regarded as archegonia which have become sterile or, with TREUB and PORSCH, as neck cells of an archegonium transformed to the egg apparatus (Fig. 552).

In some cases the mother cell of the embryo-sac does not undergo a tetrad division, but forms only three or two daughter cells or is directly transformed into the embryo-sac without dividing. The last is the case in *Lilium*, where the mature embryo-sac contains the usual eight nuclei. In *Cypripedium* and *Plumbagella*, on the other hand, the number of nuclei is reduced to four by the omission of the last

division. There may then be an egg-cell, an antipodal cell, and two polar nuclei, or alternatively in *Cypripedium* an egg-cell, two synergidae, and one polar nucleus. In all these cases the reduction division takes place in the embryo-sac, being transferred from the end of the sporophyte generation to the commencement of the gametophyte generation.

The microspores, which cannot reach the macrospore directly, germinate on the stigma (Fig. 551). The pollen-tube penetrates for the length of the style, and as a rule the tip enters the micropyle of an ovule and so reaches the apex of the nucellus. This most usual course of the pollen-tube is termed POROGAMY, but many cases of departure from it have become known of recent years.

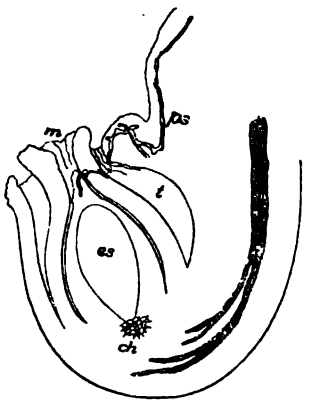


FIG. 553.—Ovule of *Ulmus pedunculata*. *es*, Embryo-sac; *m*, micropyle; *ch*, chalaza; *t*, pocket-like space between the integuments. The pollen-tube, *ps*, penetrates directly through the two integuments and reaches the apex of the nucellus. (After NAWASCHIN.)

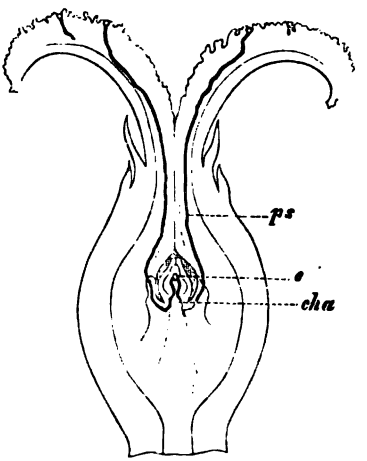


FIG. 554.—Longitudinal section of an ovary of *Juglans regia* to show the chalazogamy. *ps*, Pollen-tube; *e*, embryo-sac; *cha*, chalaza. (Somewhat diagrammatic. × 6.)

TREUB first showed in *Casuarina* that the pollen-tube entered the ovule by way of the chalaza, and thus reached the peculiar sporogenous tissue, which in this case develops a number of macrospores or embryo-sacs. CHALAZOGAMY, as this mode of fertilisation is termed in contrast to POROGAMY, has been since shown, especially by NAWASCHIN, to occur in a large number of forms. These belong to the Casuarinaceae, Juglandaceae, Betulaceae, Ulmaceae, Celtoideae, Urticaceae, Cannabinaceae, and Euphorbiaceae, which all have the common character of the pollen-tube growing within the tissues, and avoiding entrance by the micropyle. This in some cases (Urticaceae) becomes closed or, as in the Euphorbiaceae, is covered by the obturator. The pollen-tube makes its way to the embryo-sac sometimes from the chalazal end and sometimes from the side of the ovule (Fig. 553),

penetrating the tissues that lie between it and the egg apparatus. Since, according to the opinion of many authors, the families mentioned above stand at the lower end of the series of Dicotyledons where a connection with the Gymnosperms might be looked for, this type of fertilisation may be regarded as departing from the behaviour of the more numerous porogamic Angiosperms and approximating to the original relations in Gymnosperms. In the latter the whole overlying tissue of the nucellus has to be penetrated by the pollen-tube to reach the embryo-sac (Figs. 545, 553, 554).

In a more recent work NAWASCHIN shows that there are also indications in the development of the contents of the pollen-tube that these forms are at a lower stage than the majority of Angiosperms. In *Juglans* the two generative nuclei remain enclosed by a common protoplasmic mass (Fig. 555) which even enters the embryo-sac; it then gradually disappears and the naked nuclei emerge and fulfil their respective functions. NAWASCHIN points out that these relations agree with what is found in many Gymnosperms. Thus they afford a further clear indication that the transition from the latter group is to be looked for in these lower families of the Angiosperms.

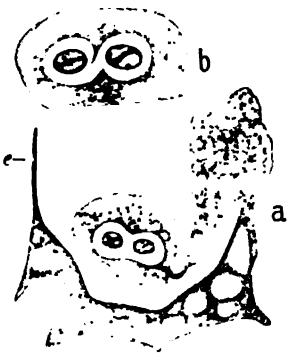


FIG. 555.—*Juglans nigra*. *a*, Part of the embryo-sac in longitudinal section before fertilisation, showing the relation of the binucleate generative cell to the egg-cell (*e*). *b*, The generative cell more highly magnified. (After NAWASCHIN.)

When the pollen-tube, containing the two generative cells, has reached the embryo-sac, its contents escape and pass by way of one of the synergidae to the ovum; the corresponding synergida then dies. One of the two generative nuclei fuses with the nucleus of the ovum, which then becomes surrounded by a cellulose wall. The second generative nucleus passes the ovum and unites with the large secondary nucleus of the embryo-sac to form the ENDOSPERM NUCLEUS (Figs. 556, 557). Both the male nuclei are often spirally curved like a corkscrew, and NAWASCHIN, who first demonstrated the behaviour of the second generative nucleus, compares them to the spermatozoids of the Pteridophyta. The further development usually commences by the division of the endosperm nucleus, from which a large number of nuclei lying in the protoplasm lining the wall of the embryo-sac are derived. The endosperm arises by the formation of cell walls around these nuclei and their proper surrounding protoplasm, and by the increase in number of the cells thus formed (Fig. 565 *A*) to produce a massive tissue.

The distinctive feature of the development of the endosperm in Angiosperms from the prothallus of Gymnosperms lies in the

interruption which occurs in the process in the case of the endosperm. In the embryo-sac, when ready for fertilisation, only an indication of the prothallus exists in the vegetative, antipodal cells. The true formation of the endosperm is dependent on the further development of the embryo-sac, and waste of material is thus guarded against. The starting-point of this endosperm formation is given by the secondary nucleus of the embryo-sac, which needs to be stimulated

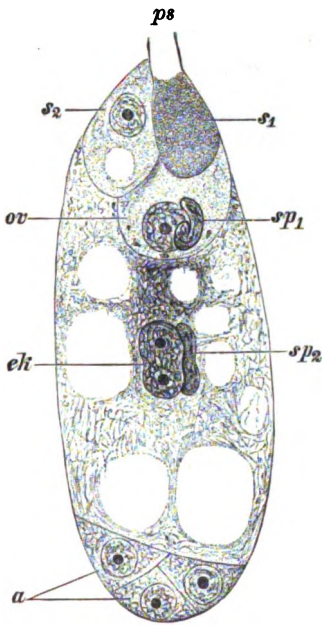


FIG. 556.—Fertilisation of *Lilium Martagon*. One of the male nuclei is close to the nucleus of the ovum, the other is in contact with the nuclei of the embryo-sac. Lettering as in Fig. 557. (Diagrammatic.)

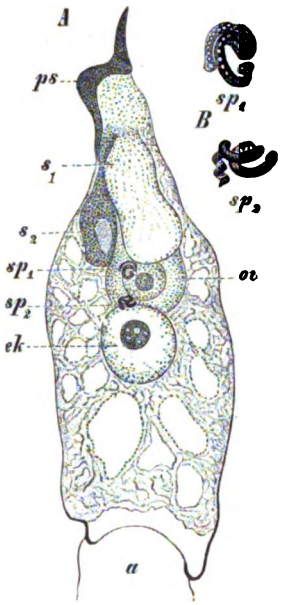


FIG. 557.—*A*, Embryo-sac of *Helianthus annuus* (after NAWASCHIN). *B*, The male nuclei more highly magnified. *ps*, Pollen-tube; s_1, s_2, synergidae; sp_1, sp_2, male nuclei; *ov*, egg-cell; *ek*, nucleus of embryo-sac; *a*, antipodal cells.

by fusion with the second generative nucleus to form the endosperm nucleus, before it enters on active division.

From the fertilised ovum enclosed within its cell wall a PRO-EMBRYO consisting of a row of cells is first developed; the end cell of this row gives rise to the greater part of the EMBRYO (9). The rest of the pro-embryo forms the SUSPENSOR. Between the embryo and suspensor is a cell known as the HYPOPHYSIS, which takes a small part in the formation of the lower end of the embryo. The segmentation of the embryo presents differences according to whether the plant belongs to the Monocotyledons or Dicotyledons. IN THE LATTER, TWO COTYLEDONS ARE FORMED AT THE END OF THE GROWING

EMBRYO (Fig. 558), AND THE GROWING POINT OF THE SHOOT ORIGINATES AT THE BASE OF THE DEPRESSION BETWEEN THEM. MONOCOTYLEDONS, ON THE OTHER HAND, HAVE A SINGLE LARGE TERMINAL COTYLEDON, THE GROWING POINT BEING SITUATED LATERALLY (Fig. 559). In both cases the root is formed from the end of the embryo which is directed towards the micropyle; its limits can be readily traced in older embryos.

After fertilisation a considerable accumulation of reserve materials is necessary in the embryo-sac both for the development of the embryo and for its future use. It is thus of importance that a means of transfer of these materials should exist. In the simplest cases the endosperm simply enlarges, crushing the surrounding tissues of the nucellus; often the antipodal cells, which are the structures which lie nearest to the chalaza, are entrusted with the function of

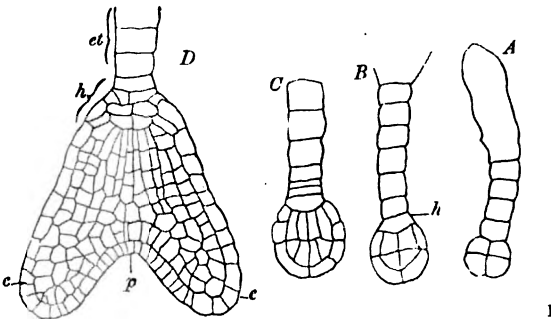


FIG. 558.—Stages in the development of the embryo of *Capsella bursa pastoris* (*A-D*). *h*, Hypophysis; *et*, suspensor; *c*, cotyledons; *p*, plumule. (After HANSTEIN, magnified.)

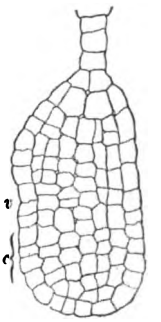


FIG. 559.—Young embryo of *Alisma Plantago*. *c*, Cotyledon; *v*, growing point. (After HANSTEIN, magnified.)

nourishing the embryo-sac. They then increase in number and sometimes undergo considerable further development. Other portions of the embryo-sac may grow out as long haustoria which sometimes emerge from the micropyle and sometimes penetrate the tissue beneath the chalaza. In some cases, especially in insectivorous and semi-parasitic plants, a special store of reserve material is laid up in this position for transference to the macrospore (Fig. 560).

A further departure in the mode of development of the embryo-sac and embryo is met with in some plants which live under quite peculiar conditions of life, such as the Podostemaceae which occur in rushing mountain streams in tropical and sub-tropical regions. In this case during the short dry period the immature flowers rapidly develop at the cost of material which has been previously stored up. Pollination, fertilisation, and the development of the seed are rapidly effected in a shortened form, so that on the return of the aquatic conditions the ripe seeds find the conditions for germination and serve to multiply and spread the plants.

In some cases plants have more or less completely lost the capacity for sexual reproduction, which has been replaced by other

modes of reproduction that can often be distinguished only by careful investigation. In place of the various expressions used by STRASBURGER and WINKLER which involve obscurity, the definitions

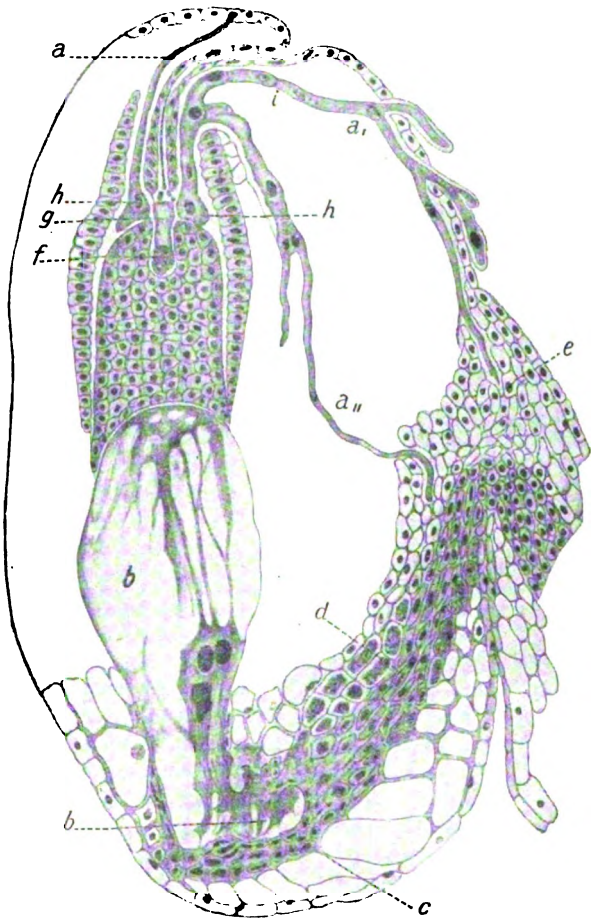


FIG. 560.—Haustoria of the embryo-sac of *Melampyrum nemorosum* (after BALICKA-IWANOWSKA). *b*, Haustoria of the chalazal end; *c*, nutritive tissue; *d*, branch of the vascular bundle; *e*, funicle; *f*, embryo; *g*, the suspensor; *a*, a_I, a_{II} haustorial tubes arising early from the micropylar end, spreading widely in the funicle and sometimes penetrating the epidermis; *h*, the base of attachment of these; *i*, cross-walls in the tubes.

of A. ERNST ([10]) may be employed. According to him PARTHENOGENESIS is the apomictic (*i.e.* resulting without fertilisation) development of gametes (especially egg-cells) of a sexually differentiated and sexually functional plant or animal, whether the process is autonomous

or induced by external conditions. It occasionally alternates with sexual reproduction, especially in lower plants in which the reduction division follows on the union of the gametes, and results from the influence of external conditions on the gametes.

APOGAMY, on the other hand, is the obligate apomictic formation of an embryo from cells of a diploid or heteroploid gametophyte. Ovogenic apogamy is when the young plant arises without a sexual process from the egg-cell. Somatic apogamy is when it arises from other cells of the gametophyte. APOSPORY is the complete omission of spore formation.

Thus in Fig. 561 a case of the apomictic development of adventitious embryos is represented. Vegetative growths from synergidae or from adjoining cells of the nucellus form in the embryo-sac and affect or completely prevent the development of the fertilised egg. Nucellar

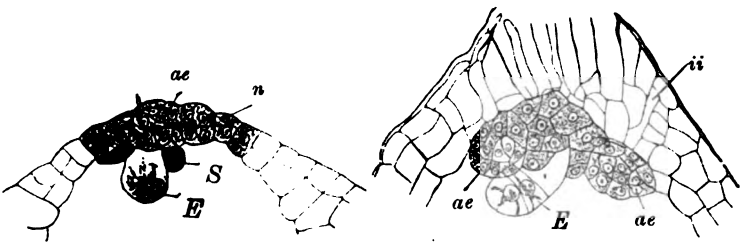


FIG. 561.—Vegetative formation of embryos in *Funkia ovata*. *n*, Nucellus with cells in process of forming the rudiments (*ae*) of the adventitious embryos; *S*, synergidae; *E*, egg-cells, in the figure on the right developing into an embryo; *ii*, inner integument. (After STRASBURGER.)

embryos of this kind are formed only after the stimulus of pollination in *Funkia* and *Citrus aurantium*. In the well-known Euphorbiaceous plant *Caelebogyne ilicifolia*, which occurs in cultivation in female specimens only, and in species of *Calycanthus*, it takes place without this stimulus. In these two latter cases we have complete loss of sexuality and somatic apogamy. Numerous cases of ovogenic apogamy have been discovered of recent years. In *Alchemilla*, *Thalictrum*, *Taraxacum*, etc., the pollen grains are usually functionless and the reduction of chromosomes in the development of the embryo sac is suppressed, so that the nuclei retain the diploid number of chromosomes; the plants have become apogamous. According to the investigations of OSTENFELD and ROSENBERG, the genus *Hieracium* is of special interest, since the formation of the embryo within the ovule may commence in very various ways. In most cases a tetrad formation accompanied by a reduction division takes place, but only some of these ovules are found to have a normal embryo-sac capable of fertilisation; as a rule this is displaced by a vegetative cell which develops into an embryo-sac aposporously (Fig. 562). In exceptional cases apogamous embryo-sacs are formed.

The Seed

The entire structure developed from the ovule after fertilisation is termed the SEED. Every seed consists of the more or less advanced EMBRYO developed from the fertilised ovum, the ENDOSPERM surrounding the embryo, and the protective SEED-COAT. The seed-coat always is derived from the integument or integuments; their cells, by the thickening, suberisation, and lignification of the walls, give rise to an effective organ of protection against drying and injury for the dormant young plant within. A special development of the epidermis of the seed into mucilage cells is of frequent occurrence (Quince, *Linum*, many Cruciferae, etc.). The mucilage serves as a first means of fixation in the soil and also retains water which is necessary for germination. Such other features of the surface as hairs, prickles, etc., have usually the former function, if they do not stand in relation to the distribution of the seed.

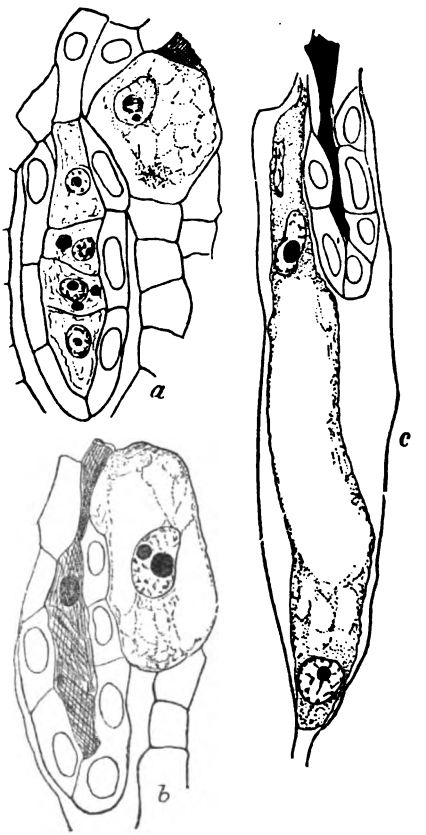


FIG. 562.—Aposporous origin of the embryo-sac of *Hieracium flagellare*. *a*, Normal tetrad of macrospores; *b*, *c*, the disorganisation of this. The diploid embryo-sac arises from a cell of the integument that is recognisable in *a*. (After ROSENBERG and A. ERNST, 1918.)

Points of morphological importance in the seed-coat are (1) the MICROPYLE, (2) the HILUM (= place of attachment to the funicle), and (3) the RAPHE. From what was said above (p. 540) it follows that the micropyle and hilum will lie at opposite poles of the seed when the ovule is atropous (Fig. 508). In seeds derived from anatropous ovules (*i.e.* those in which the funicle lies along one side of the ovule, which is bent round at the chalaza) the hilum and micropyle are close together. Only seeds of this kind possess a raphe connecting the hilum and chalazal region. Campylo-

tropous ovules develop into seeds resembling those derived from anatropous ovules, but the embryo is curved.

In some cases the function of the seed-coat is modified owing to the protection of the seed or seeds being undertaken by the pericarp; this or its innermost layers are developed as sclerotic cells and form the stone of the drupe or shell of the nut. In such cases (*e.g.* Almond, Cherry-Laurel, Cherry, Pepper, etc.), since any special development of the seed-coat is unnecessary, it tends to become reduced; its cells do not thicken or modify their walls and the various layers become simply compressed.

The nutritive tissue in the seeds is developed, in the case of Gymnosperms (except in *Gnetum*), by the time of fertilisation and

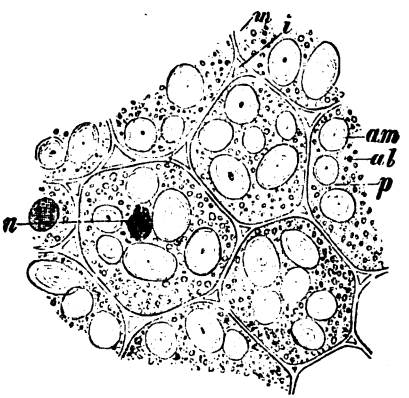


FIG. 563.—Part of section through one of the cotyledons of the Pea, showing cells with reserve material. *am*, Starch grains; *al*, aleurone grains; *p*, protoplasm; *n*, nucleus. (× 160. After STRASBURGER.)

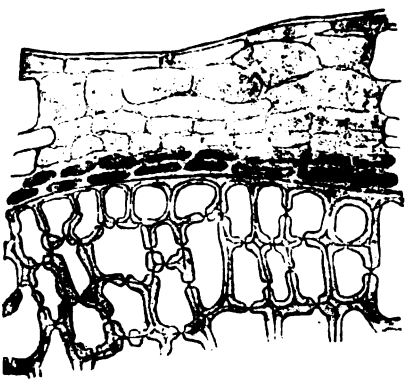


FIG. 564.—Transverse section of the seed of *Colchicum*, showing the reserve-cellulose of the endosperm within the seed-coat.

constitutes the prothallium (cf. p. 565). This fills the embryo-sac and nourishes the embryo, which grows down into it. The surrounding tissue of the nucellus becomes crushed so that the embryo-sac extends to the seed-coat. The cells of the endosperm are packed with reserve materials (starch, fat, proteid), and these are utilised in the further development of the embryo; this takes place on germination, usually after a period of rest.

The nutritive tissue in the Angiosperms (and of *Gnetum*) arises, on the other hand, after the egg-cell has been fertilised. It originates from the secondary nucleus of the embryo-sac derived by the fusion of the two polar nuclei. This is stimulated to division after fusion with the second generative nucleus. The nuclei produced by this process of division are distributed in the protoplasm which lines the wall of the embryo-sac, and when a large number has been formed the

protoplasm divides to form numerous cells. These by further division fill the whole embryo-sac with the tissue of the endosperm.

In Angiosperms also the endosperm as a rule compresses the remains of the nucellus. Reserve materials such as starch, fatty oil, and aleurone grains are accumulated in the cells (Fig. 563); in other cases the greatly thickened walls form a store of reserve cellulose

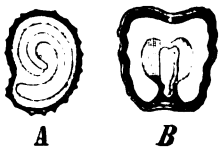


FIG. 565.—*A*, Seed of *Hyoscyamus niger*, showing the dicotyledonous embryo embedded in the endosperm; *B*, seed of *Elettaria Cardamomum*, enveloped by a thin aril; the white, mealy perisperm next to the seed-coat encloses an oleaginous endosperm (shaded), in which the monocotyledonous embryo lies embedded. (After BERG and SCHMIDT.)

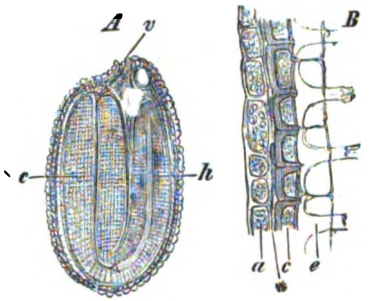


FIG. 566.—*Capsella bursa pastoris*. *A*, Longitudinal section of a ripe seed; *h*, hypocotyl; *c*, cotyledons; *v*, vascular bundle of the funicle (× 26). *B*, Longitudinal section of the seed-coat after treatment with water; *e*, the swollen epidermis; *c*, brown, strongly thickened layer; *, compressed layer of cells; *a*, the single persisting layer of endosperm cells containing aleurone grains. (× 250. After STRASBURGER.)

(Fig. 564). In a few cases, as in Piperaceae, Scitamineae, etc., the nucellus persists and also serves as a nutritive tissue; it is then

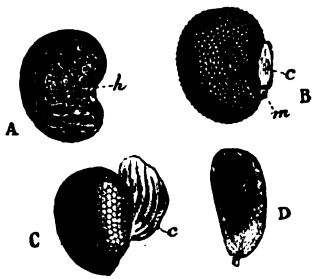


FIG. 567.—*A*, Seed of *Papaver Rhoeas*; *h*, the hilum. *B*, Seed of *Corydalis ochroleuca*; *m*, micropyle; *c*, caruncula. *C*, Seed of *Chelidonium majus*. *D*, Seed of *Nymphaea alba* with its arillus. (After DUCHARTRE.)

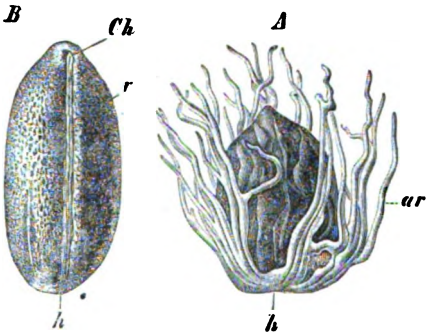


FIG. 568.—*A*, *Myristica fragrans*, seed from which the arillus (*ar*) is partly detached. *B*, *Myristica argentea*, seed after removal of the arillus; *Ch*, chalaza; *r*, raphe; *h*, hilum. (After WARBURG. ½ nat. size.)

termed PERISPERM (Fig. 565 *B*). When lamellae of the perisperm or of this and the seed-coat grow into the endosperm, they usually differ from the latter in colour and contents; the endosperm is then said to be ruminated (*Myristica*, *Areca*).

In very many cases, *e.g.* Leguminosae Cruciferae, etc., not only is the nucellus absorbed by the endosperm, but the latter is completely displaced by the embryo. The reserve materials are then stored up in the cotyledons or in the whole body of the embryo (Fig. 566).

Lastly, a structure known as the ARILLUS must be mentioned, which usually stands in relation to the distribution of the seeds. It arises as a succulent and usually brightly coloured outgrowth from the funicle. It grows up around the ovule and ultimately comes to invest the seed more or less completely (Figs. 567 *D*, 568, 586). An outgrowth in the neighbourhood of the micropyle, which is found in the Euphorbiaceae, is termed a CARUNCULA (Fig. 567 *C*, *B*).

The Fruit (11)

The effect of fertilisation is not only seen in the macrosporangia but extends to the macrosporophylls or carpels. The structures of very various form which are formed from the carpels (often together with the persistent calyx and the floral axis) are called FRUITS, and serve primarily to protect the developing seeds. In Gymnosperms, where the ovules are borne freely exposed on the carpels, no fruits in the strict sense can exist, since no ovary is present. Thus in *Cycas*, *Ginkgo*, *Taxus*, *Podocarpus*, *Gnetum*, and *Ephedra* we can only speak of seeds and not of fruits. When, however, the carpels after fertilisation close together as in the cones of some Gymnosperms and the berry-like cones of *Juniperus*, a structure analogous to the angiospermic fruit is formed, and the term fruit may be used.

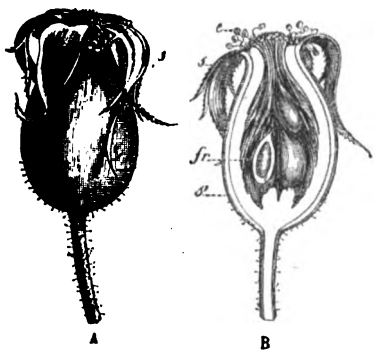


FIG. 569.—Collective fruit of *Rosa alba*, consisting of the fleshy hollowed axis *s'*, the persistent sepals *s*, and the carpels *fr*. The stamens *e* have withered. (After DUCHARTRE.)

A great variety in the development of the fruit in Angiosperms might be anticipated from the range in structure of the gynaeceum described above. The simplest definition of a fruit is the ripened ovary, but difficulties arise in the case of apocarpous gynaecea.

The product of the individual carpels associated in such apocarpous gynaecea as those of the Rosaceae will here be termed PARTIAL FRUITS or FRUITLETS, while the product of the whole gynaeceum will be spoken of as the FRUIT or the COLLECTIVE FRUIT. The hollowed-out or projecting floral axis bearing the carpels may be included in the fruit. Thus the Strawberry is a collective fruit composed

of the succulent receptacle bearing the small yellow nut-like fruitlets. In the Apple the core only is the fruit, the succulent tissue being derived from the hollowed floral axis surrounding and fused with the carpels. In the *Rose* there is similarly a collective fruit, the fruitlets being the hard nutlets enclosed by the succulent receptacle (Fig. 569). In the case of fruits resulting from syncarpous gynaecea the further development of the wall of the ovary as the PERICARP has to be especially considered. The outermost, middle, and innermost layers of this are

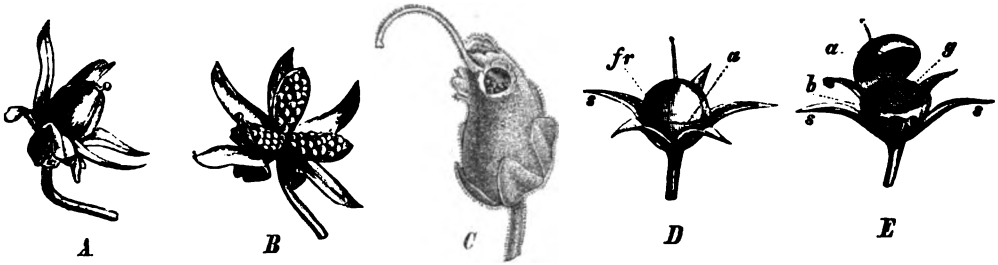


FIG. 570.—Modes of dehiscence of capsular fruits. *A*, *B*, Capsule of *Viola tricolor* before and after the dehiscence; *C*, poricidal capsule of *Antirrhinum majus* (magnified); *D*, *E*, pyxidium of *Anagallis arvensis* before and after dehiscence.

distinguished as EXOCARP, MESOCARP, and ENDOCARP respectively. According to the nature of the pericarp the forms of fruit may be classified as follows:

1. A fruit with a dry pericarp, which opens when ripe, is termed a CAPSULE (Fig. 570).

When dehiscence takes places by a separation of the carpels along their lines of union the capsule is SEPTICIDAL; when the separate loculi open by means of a longitudinal split, it is termed LOCULICIDAL, and when definite circumscribed open-

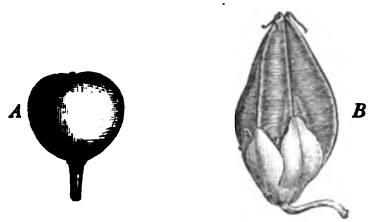


FIG. 571.—Dry indehiscent fruits. *A*, Nut of *Fumaria officinalis* (× 6). *B*, Achene of *Fagopyrum esculentum* (× 2). (After DUCHARTRE.)

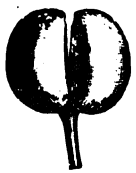


FIG. 572.—Schizocarp of *Galium mollugo*. (× 6. After DUCHARTRE.)

ings are formed, it is termed PORICIDAL. As special types of frequent occurrence may be mentioned: the FOLLICLE, which is a capsule developed from a single carpel and opening by separation of the ventral suture, *e.g. Aconitum* (Fig. 644); the LEGUME or pod, which differs from the follicle in dehiscing by both ventral and dorsal sutures, *e.g. Laburnum* (Fig. 711).

2. DRY INDEHISCENT FRUITS have a dry pericarp which does not open at maturity. Those with a hard pericarp are termed NUTS, *e.g.* Hazel-nut, Lime (Fig. 669), *Helianthus* (Fig. 784 *A*).

3. When a dry fruit, consisting of several carpels, separates at maturity into its partial fruits without the latter opening, it is termed a SCHIZOCARP (*e.g.* Umbelliferae, *Malva*, *Galium*, Fig. 572).

4. A BERRY (Fig. 573) is a fruit in which all the layers of the pericarp become succulent, as in *Vaccinium*, *Vitis*, etc.

5. In the DRUPE the pericarp is differentiated into a succulent exocarp and a hard endocarp. *Prunus Cerasus* (Fig. 697) and *Juglans regia* (Fig. 602) are familiar examples.

When, on the other hand, the group of fruits borne on an inflorescence has the appearance of a single fruit, the structure may be termed a SPURIOUS FRUIT. The Fig (*Ficus*) is the best-known example of this, but similar spurious fruits are especially frequent in the Urticaceae and Moraceae. The comparison of a Blackberry which is the product of a single flower with the spurious fruit of the Mulberry will show how closely the two structures may resemble one another (Fig. 574).

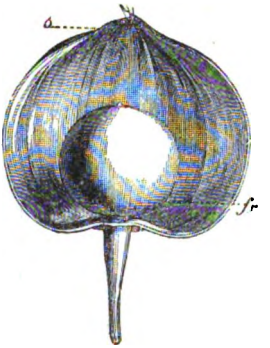


FIG. 573.—Fruit of *Physalis alkekengi*, consisting of the persistent calyx *s*, surrounding the berry *fr*, derived from the ovary. (After DUCHARTRE.)

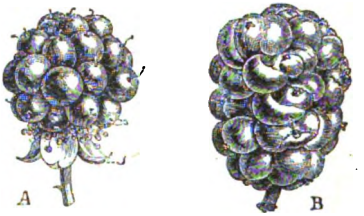


FIG. 574.—*A*, Collective fruit of *Rubus fruticosus*, consisting of a number of drupes. *B*, Inflorescence of Mulberry (*Morus nigra*) bearing a number of small drupes. (After DUCHARTRE.)

Distribution of Seeds (12)

The most important means by which Spermatophytes compete with others living under the same conditions is to produce as many seeds as possible. With the number of descendants the probability that some at least will succeed is increased. The number of seeds by itself would, however, be of little avail if all the seeds remained in the place of their origin. Thus good arrangements for the distribution of the seeds are of the greatest importance, and the form and construction of fruits and seeds exhibit the great influence of this factor.

The same agents are available in the distribution of seeds as in the conveyance of pollen—currents of air and water, animals, and in addition human traffic. A distinction must be made, however, between the conveyance of pollen and of seeds, in that while a pollen grain is

extremely small and weighs very little, seeds contain a certain amount of reserve materials and are thus larger and heavier. In spite of this the transport of seeds by the wind is the main means of their dispersal.

Often the suitability of seeds for wind-dispersal is due simply to their minute size and their lightness; thus millions of seeds are produced in a capsule of *Stanhopea*, and the weight of a seed of *Dendrobium attenuatum* has been determined to be about $\frac{1}{10}$ milligramme. Thus these Orchids play a part as epiphytes in damp tropical forests only equalled by Ferns, the spores of which are as light. A much more common arrangement is found in heavier seeds when the volume is increased and a large surface is offered to the wind. Either the whole surface of the seed bears longer or shorter hairs as in the Willow (Fig. 611), Poplar (Fig. 612), and Cotton (Fig. 667), or a longer tuft of hairs is borne at one end as in the Asclepiadaceae and Apocynaceae (*Strophanthus*, Fig. 745), and many Gesneriaceae and Bromeliaceae. An equally frequent arrangement in other families of plants is

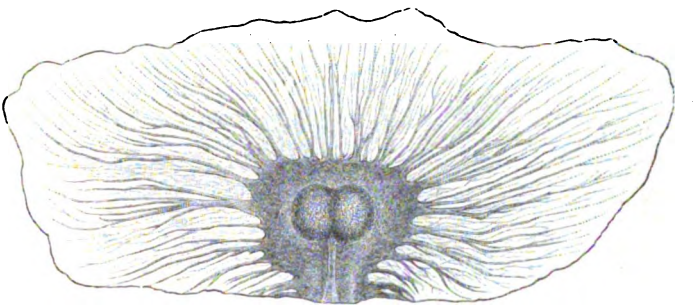


FIG. 575.—Winged seed of *Pithecoctenium echinatum*. (After NOLL. Nat. size.)

the development of a flat wing formed of a thin and light membrane. This in our Firs (Fig. 591) and Pines (Fig. 593) is split off from the ovuliferous scale, while in *Rhododendron*, Bignoniaceae, some Cucurbitaceae (*Zanonia*), and in the Rubiaceae (*Cinchona*, Fig. 766) it develops on each seed within the ovary. In no case is it more perfect than in *Pithecoctenium echinatum* (Fig. 575), where the delicate silky wing leads to the falling seed assuming an almost horizontal position and being carried far even by a slight breeze.

Other parts of the flower or fruit may be developed as wings, especially when one-seeded fruits (or schizocarps) are concerned. Examples of this are afforded by the sepals of the Dipterocarpaceae, the large bract of the inflorescence of the Lime (Fig. 669), the bract and bracteoles of *Carpinus* (Fig. 605), and more commonly the wall of the ovary as in *Betula* (Fig. 604), *Alnus*, *Ulmus* (Fig. 613), Polygonaceae (Fig. 618 *D*), *Acer* (Fig. 684), *Fraxinus* (Fig. 739), or the fruits of the Typhaceae, *Eriophorum* (Fig. 809) and *Anemone* (Fig. 641). The same use is served by the crown of hairs (pappus) which is developed at the upper end of one-seeded fruits such as those of the Valerianaceae (Fig. 769) and Compositae (Figs. 780, 785), especially when it has a parachute-like form due to the later elongation of the upper end of the fruit as in *Taraxacum*, *Tragopogon*, etc. According to DINGLER the fall in air as compared with that in a vacuum in the first second is six times slower in the case of the fruits of *Cynara Scolymus* provided

with scaly hairs; in *Pinus sylvestris* the fall is seven times and in *Pithecoctenium* thirty times slower.

The distribution of seeds and fruits by ocean currents is important for many plants. The strand-flora of the Malayan Archipelago, for example, consists, according to SCHIMPER'S investigations, exclusively of plants with floating fruits or seeds, the adaptations of which correspond more or less to those of the Coco-nut (Fig. 821) which is distributed everywhere on tropical coasts. A thick exocarp consisting of a coarsely fibrous tissue renders the fruit buoyant and protects the brittle and stony endocarp from being broken against the rocks and stones of the shore. A very similar structure is exhibited by species of *Barringtonia*, *Cerbera Odollam* (Fig. 576), *Terminalia catappa*, *Nipa fruticans*, and many smaller plants belonging to the shrubby and herbaceous vegetation of the dunes and strand. In all cases the capacity of floating for a long time is a condition of the distribution of the seeds and the success of the species.

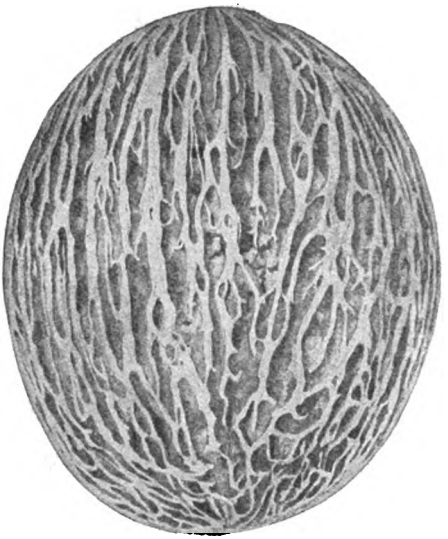


FIG. 576.—Fruit of *Cerbera Odollam*, from the drift. The succulent endocarp is wanting, so that the buoyant tissue traversed by coarse fibrous strands is exposed. (After SCHIMPER.)

The distribution of fruits and seeds by means of animals depends as a rule upon the succulent and attractive fruits serving as food for birds, the undigested seeds being shed. A familiar example is afforded by the Elder (*Sambucus nigra*), the black fruits of which are eaten by various birds in summer. There are many such cases, and for some seeds the passage through the intestine of the animal appears to be a necessary preliminary to germination. The development of an arillus (cf. p. 582) is in many cases an adaptation to distribute the seed by means of animals. The arillus of *Taxus* with its bright red colour which surrounds the single seed is greedily eaten by blackbirds; the red fruits of *Euonymus* when they open expose four seeds with bright red arilli, which are eaten by chaffinches. The Nutmeg is distributed over the islands about the Moluccas by a large pigeon which is attracted by the bright red arillus around the black seed which is exposed on the dehiscence of the fruit. In a similar way our Mistletoe in winter, when little other food can be obtained, is eaten by blackbirds and other birds; when the birds clean their beaks the seeds remain attached to the branches by reason of the viscid substance around them and are able to germinate in this position. The spread of plants with hooked fruits, etc., such as *Galium aparine*, species of *Lappa* (cf. Fig. 781), *Bidens*, *Xanthium*, etc., by means of the fur of quadrupeds, the general distribution of water-plants from one pond to another by aquatic birds, and the distribution of the Hazel-nut, etc., by means of squirrels, do not require detailed description. Lastly, the distribution of certain

seeds by means of ants must be mentioned ; these animals are attracted to remove and accumulate the seeds by the abundance of oil in the elaiosome-containing tissue of appendages such as the caruncula.

It is a matter of general knowledge that man by his commerce and industry has exerted great influence on the distribution of food-plants and other plants of economic value. In this way the seeds of many weeds have been unintentionally distributed over the inhabited earth, a fact that could be illustrated by numerous examples.

Germination [13]

Seeds which have escaped the various risks of distribution require to be soon covered with soil. Small seeds readily find shelter in cracks or depressions of the soil and become fixed there owing to special properties of their surface. Larger seeds are sufficiently covered by fallen leaves. The fruitlets of *Erodium* and other Geraniaceae, of *Avena sterilis*, species of *Stipa* and other Gramineae penetrate the soil by the aid of their hygroscopic curvatures (cf. p. 334, Fig. 275) ; the presence on their surface of backwardly-directed hairs prevents their losing the position reached. The burial of the fruits of *Arachis hypogaea*, *Trifolium subterraneum*, and *Okenia hypogaea*

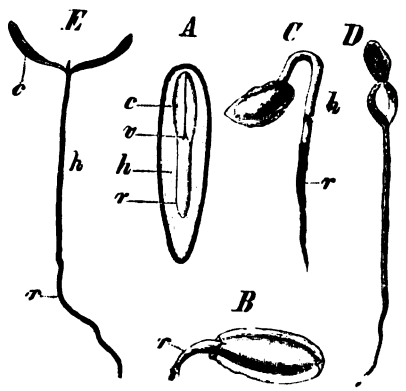


FIG. 577.—*Thuja occidentalis*. *A*, Median longitudinal section of the ripe seed. *B-E*, Stages in germination ; *h*, hypocotyl ; *c*, cotyledons ; *r*, radicle ; *v*, growing point of stem. (*A* × 5 ; *B*, *C* × 2 ; *D*, *E* nat. size. After SCHENCK.)

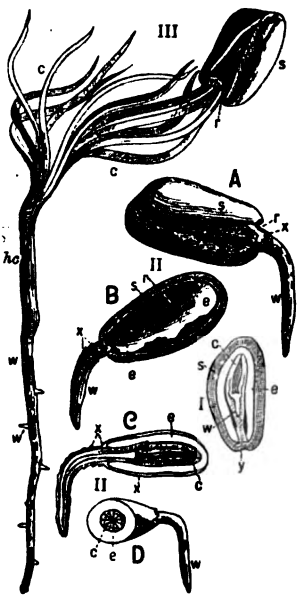


FIG. 578.—*Pinus pinea*. Germination. (After SACHS.) *I*, Longitudinal section of the seed ; *y*, micropylar end. *II*, Early stage of germination ; *s*, seed-coat ; *e*, endosperm ; *w*, primary root ; *x*, broken-through embryo-sac ; *r*, red layer of the seed-coat. *III*, The cotyledons (c) have escaped from the exhausted seed ; *hc*, hypocotyl ; *w'*, lateral roots.

is brought about by the growth of their positively geotropic stalks, while negative heliotropism determines the insertion of the fruits of *Linaria cymbalaria* into the crevices of the walls on which the plant lives (cf. p. 351).

When the seeds find sufficient moisture they swell considerably. With this

they lose some of their resistance to such dangers as extremes of temperature and desiccation; their former resistance was due to the small proportion of water they contained. The next step is the rupture of the seed-coat, which, as a rule, is effected by the emerging root. The root at once bends downwards geotropically and, by means of its root-hairs, which are especially long and numerous at the

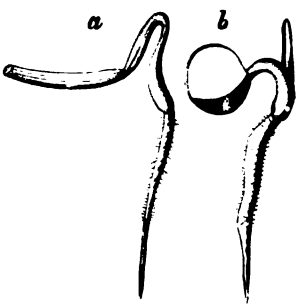


FIG. 579.—Seedlings, *a*, of *Scorzonera humilis*; *b*, of *Iris pseudacorus*. (After KLEBS.)

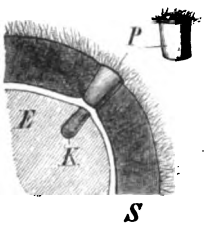


FIG. 580.—Section through the upper part of the fruit of *Acrocomia sclerocarpa*. *S*, The hard shell; *P*, the plug which is pushed out of the shell by the germinating embryo, *K*; *E*, endosperm. (After PFITZER.)

FIG. 581.—*Kandelia Rheedii*. The massive root of the seedling (*1*) has broken out of the fruit. When the plant separates from the fruit the root will become inserted into the muddy soil. (From SCHIMPER'S *Plant-Geography*.)

junction of the root and hypocotyl, fastens the seedling in the soil. Meanwhile the hypocotyl grows and gradually emerges from the seed-coat, while the cotyledons as a rule remain for a time enclosed in the latter and absorb the remainder of the reserve material (Figs. 577, 579). This process leads to the hypocotyl becoming more and more strongly curved, and the tension resulting from its further growth withdraws the cotyledons from the seed-coat. The seedling then becomes erect, the leaves are expanded and can assimilate, and thus its independent life commences. The number of cotyledons is usually 2, but in some genera of Coniferae varies from 3-∞ (Fig. 578).

This most frequent type of germination is characterised by the cotyledons being expanded above ground and is termed EPIGEAL. It is nearly always found in the case of small seeds.

HYPOGEAL germination is for the most part found in large-seeded Dicotyledons, the cotyledons of which contain the stored reserve materials (*e.g. Vicia faba*, *Pisum*, *Aesculus*, *Juglans*, etc.). It is characterised by the cotyledons remaining enclosed in the seed-coat after the root has penetrated into the soil; the epicotyledonary stem emerges from between the cotyledons, becomes erect, and bears the later leaves in the usual way. While there is a sharp morphological distinction between the two types of germination, the difference is of little systematic value; within the Papilionaceae many intermediate conditions are found, and in the genus *Phaseolus*, *Ph. vulgaris* is epigeal and *Ph. multiflorus* hypogeal.

The germination of monocotyledonous seeds differs from the cases described above in that after the main root has emerged the sheathing base of the larger or smaller cotyledon emerges from the seed. Its tip remains either for a time or permanently in the seed, and serves as an absorbent organ to convey the reserve materials stored in the endosperm to the seedling. The first leaf of the latter soon emerges from the sheathing base of the cotyledon (Fig. 579 *b*). Very hard seed-coats are often provided with special arrangements to enable the root to escape. Thus in the coco-nut three openings are present, one corresponding to each carpel. The opening behind which the tip of the root of the single embryo is situated is covered by a very thin layer, while the two other openings are firmly closed. The hard stony seed-coat of another Palm (*Acrocomia sclerocarpa*) (Fig. 580) has a loosely fastened plug opposite the tip of the root. In the whole family of the Scitamineae there is a limited thinner region of the hard seed-coat above the root-tip of the embryo, which is lifted up as a sort of lid on germination.

The so-called "viviparous" plants show peculiar arrangements which can only be briefly mentioned here (Fig. 581). Vivipary is found in the inhabitants of tropical mangrove-swamps and is to be regarded as an ecological adaptation to the conditions of life. The one-seeded fruits germinate while still attached to the parent plant, *i.e.* the pericarp is ruptured by the radicle of the embryo which first grows from the micropylar end of the seed. The hypocotyl which thus becomes free may attain the length of over 1 metre in *Rhizophora* (cf. Fig. 716). This swells somewhat in the lower part, and the embryo thus hangs by its absorbent cotyledons which remain in the seed, until it separates from the plant owing to its own weight, and, falling vertically, sticks into the soft mud.

Arrangement of the Classes, Orders, and Families

CLASS I

Gymnospermae (14)

Order 1. Cycadinae

This includes the single Family **Cycadaceae**. These are woody plants restricted to tropical and sub-tropical regions. *Cycas* is a native of Asia; *Macrozamia* and *Bowenia* of Australia. *Encephalartos* and *Stangeria* are African, while America has the genera *Dioon*, *Ceratozamia*, *Zamia*, and *Microcycas*. The stem, which undergoes secondary growth in thickness, is as a rule unbranched or forms a sympodium, and bears large, pinnate foliage leaves. These, which are

of firm leathery texture and persist for a number of years, alternate with smaller scale leaves and form a large terminal crown. The surface of the cylindrical or tuberous stem is clothed with the scale leaves and the bases of the old foliage

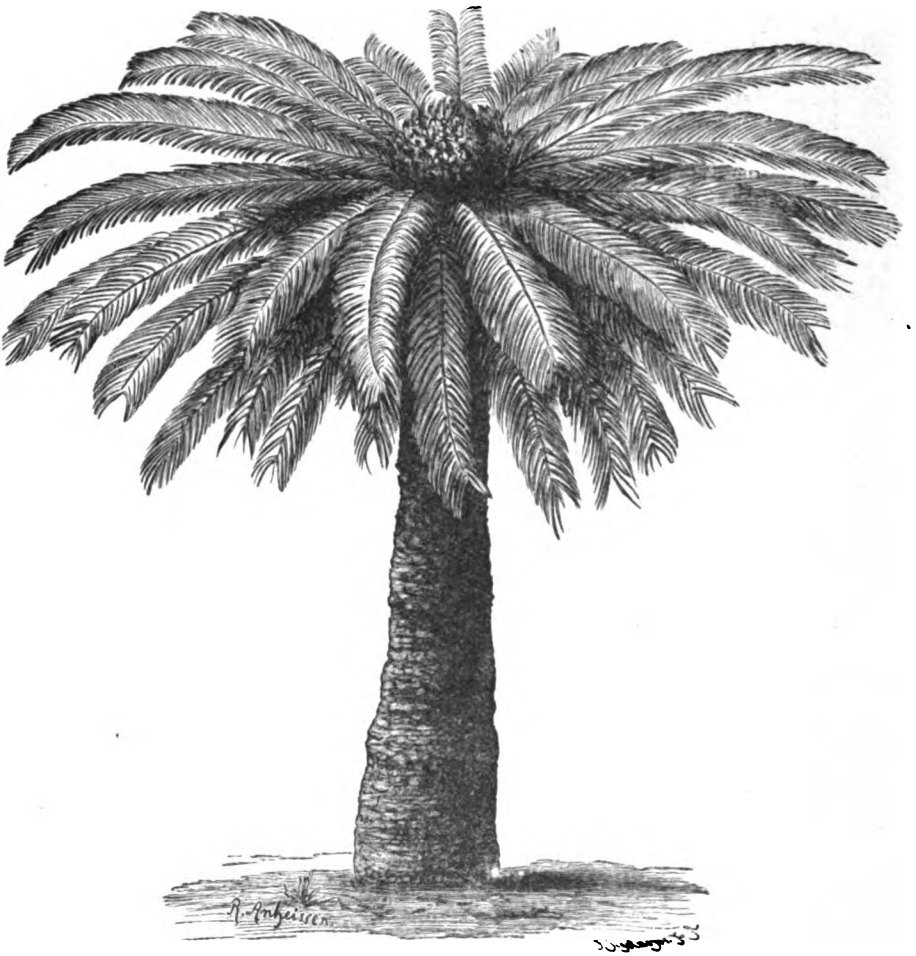


FIG. 582.—*Cycas revoluta*, female plant in flower. (From a photograph.)

leaves. Mucilage ducts are present in all parts of the plant. The vascular bundles are collateral, but their xylem consists of tracheides only.

The Cycadaceae are dioecious. Fig. 582 represents a female plant of *Cycas revoluta*, in which the growing point forms alternate zones of foliage leaves and macrosporophylls. When young the foliage leaves are rolled up circinately as in the Ferns. One of the sporophylls is represented in detail in Fig. 582*a*. It shows the pinnate form of the foliage leaf, but is densely covered with brown hairs,

and chlorophyll is wanting. Towards the base two to eight macrosporangia are borne on the margins, in the place of pinnae. It is evident that each female plant of *Cycas* which has reached the flowering condition exhibits a regular succession of flowering and vegetative periods. The flower represented by the group of sporophylls is always grown through by the further development of the apex which does not branch. The male plant of *Cycas* and the other Cycadaceae bear their sporophylls in terminal cones often of great size, while the further growth of the plant is effected by a lateral bud which continues the direction of growth of the sympodial axis, displacing the cone to one side.

FIG. 582*a*.—Macrosporophyll (Carpel) of *Cycas revoluta*.

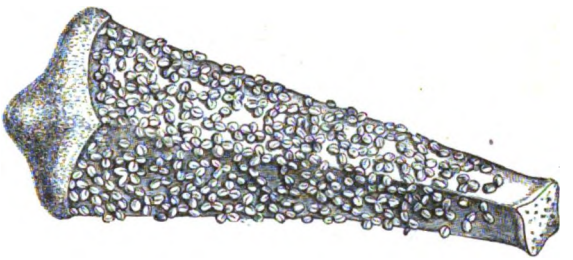


FIG. 582*b*.—Microsporophyll (stamen) of *Cycas circinalis*.

The cones consist of numerous sporophylls arranged spirally on the axis. The microsporophylls bear large numbers of microsporangia on the lower surface (Fig. 582*b*). The macrosporophylls of the cone-bearing Cycadaceae are considerably modified as compared with *Cycas*, and each bears two marginal macrosporangia (Fig. 583). For the developmental history cf. p. 562.

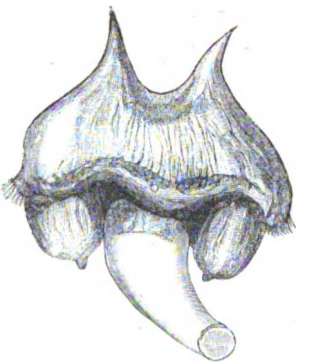


FIG. 583.—*Ceratozamia robusta*. Macrosporophyll with two macrosporangia. (After GOEBEL.)

Order 2. Ginkgoinae

The single representative of the Family of the **Ginkgoaceae** which forms this order is *Ginkgo biloba*. This tree comes from Japan, but is often seen in cultivation in Europe. The long-stalked leaves are divided dichotomously into two or more lobes and are shed annually. The flowers are dioecious. The numerous stamens are situated on an elongated axis which bears no enveloping leaves. Microsporangia with an "endothecium" (cf. p. 546). Macrosporangia in pairs at the summit of short shoots; sporophylls reduced to a collar-like outgrowth around the base of the sporangium (Fig. 584). Developmental history, cf. p. 562.

Order 3. Coniferae

The Coniferae include conspicuous trees or shrubs with woody stems. The possession of small, undivided, firm leaves, flat or needle-shaped, of xerophilous structure, and usually lasting for several seasons, is a common character of the plants of the order; they thus with a few exceptions, such as the Larch, belong to the evergreen vegetation. All Conifers are profusely branched, and a distinction into long and short shoots is evident in the genera *Pinus*, *Larix*, and

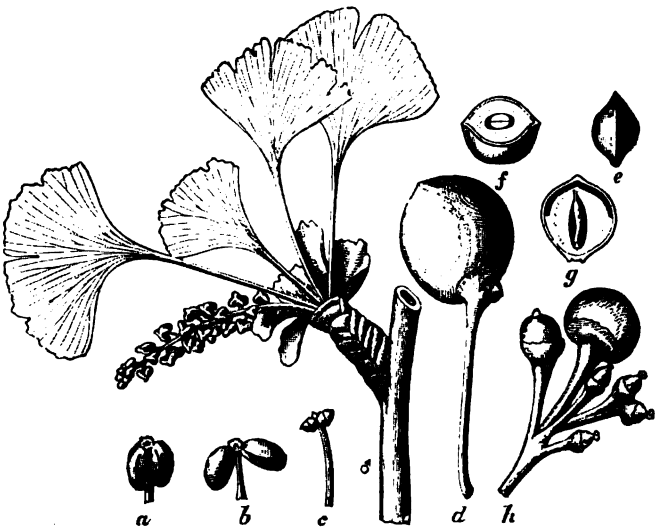


FIG. 584.—*Ginkgo biloba*. Male branch with flower; the leaves are not yet full-grown. *a*, *b*, Stamens; *c*, female flower; *d*, fruit; *e*, stone of same; *f*, stone in cross section; *g*, in longitudinal section showing the embryo; *h*, female flower with an exceptionally large number of ovules borne on separate stalks. (Male flower and *c*, nat. size; *d*, slightly reduced; the other figures magnified. After RICHARD; *a-d* after EICHLER.)

Cedrus. In all cases the direction and rapidity of growth of the main axis differs from that of the lateral branches. This is especially seen in young individuals; old trees are often more irregular in outline.

The absence of vessels from the xylem of young plants and from the secondary wood is an anatomical characteristic (cf. p. 151). Their place is taken by large tracheides with peculiar bordered pits on the radial walls; these form a very uniform wood. The majority of the Coniferae have resin abundantly present in all the parts of the plant.

The Coniferae in contrast to the Cycadinae are mostly inhabitants of temperate regions, and are among the trees which approach nearest to the polar regions. Within the tropics they are mostly confined to mountains.

The Coniferae are divided into two families on account of differences in the floral structure.

The *Taxaceae* have female flowers with one or few macrosporangia; the latter are usually provided with an arillus. The flowers are usually not definite cones. Mostly dioecious.

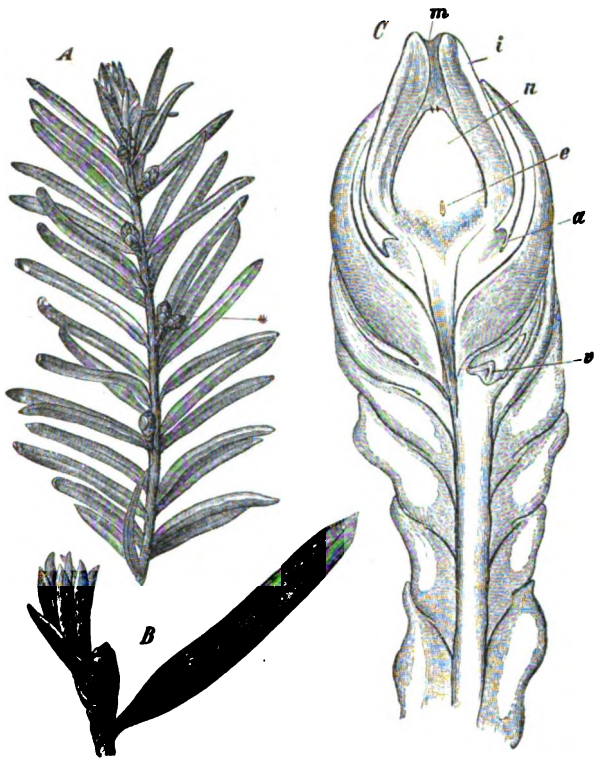


FIG. 585.—*Taxus baccata*. *A*, branch with female flowers; *, two ovules on the same shoot (nat. size). *B*, Leaf with axillary, fertile shoot (× 2). *C*, Median longitudinal section of a primary and secondary shoot; *r*, vegetative cone of the primary shoot; *a*, rudiment of the aril; *e*, rudiment of the embryo-sac; *n*, nucellus; *i*, integument; *m*, micropyle (× 48). (After STRASBURGER.) *Poisonous.*

The *Pinaceae*, on the other hand, have a number of ovules in each female flower, the latter being a cone with numerous sporophylls borne on an axis. Arillus not present. Usually monoecious.

Family **Taxaceae**.—The plants belonging to this family are grouped in a number of small genera distributed in the southern hemisphere. The most important genus is *Podocarpus*, the numerous species of which are widely distributed in temperate East Asia and in Australia and New Zealand, and also occur as stately trees on the mountains of the Asiatic tropics. The female flowers are small shoots,

the sporophylls of which are swollen and succulent ; one or two sporophylls bear at the summit a single anatropous ovule surrounded by a fleshy arillus. The male flowers, which are borne on the same or on distinct individuals, are small cones consisting of numerous sporophylls attached to a short erect axis. Each sporophyll bears two microsporangia on the lower surface ; the microspores are provided with distended wings.

Taxus baccata is the only European representative of the family. The Yew, which is now for the most part artificially introduced, had formerly a wide distribution as an evergreen undergrowth in our native woods (Figs. 585, 586). The Yew tree attains a height of 10 m. Isolated examples of large size occur. All

FIG. 586.—*Taxus baccata*, bearing fruits. (½nat. size.) *Poisonous.*

the branches are shoots of unlimited growth. The leaves stand on all sides of the ascending main shoots, but in two rows on the horizontally-expanded lateral branches. They are narrow, flat leaves and persist for several years. The tree is dioecious ; the flowers are situated on the lower surface of the twigs and arise in the axils of the leaves of the preceding year. The male flowers are invested at the base by a number of scale leaves and contain some 10 peltate stamens, each of which bears 5-9 pollen sacs. The mode of opening of the sporangia is peculiar. The outer wall splits at the base and along the side of each pollen-sac, so that the whole stamen resembles an umbrella turned inside out ; the pollen remains for a time in the pocket-like depressions, from which it is removed by the wind. The female flower usually develops singly as a secondary, axillary shoot of the uppermost

scale leaf of a primary shoot; the apex of the latter is displaced to the side and does not develop further. Each flower consists of a single, atropous ovule with

FIG. 587.—*Juniperus communis*. Twigs bearing fruits and male flowers. ½ nat. size.) OFFICIAL. *A*, Male flower; *B*, fertile shoot with female flower; *C*, female flower with one scale bent out of place; *D*, fruit. (All magnified. After BERG and SCHMIDT.)

one integument. The drop of fluid excreted from the micropyle of many Gymnosperms is especially well shown by the Yew. As the seed develops, a fleshy arillus springs from its base and surrounds the mature seed like a bright red cup. The

foliage and seed are poisonous, but the aril, which induces birds to distribute the seed, is harmless.

Family **Pinaceae**.—This family includes the most important Coniferae, and on grounds of differences in leaf arrangement and in the position of the ovules is divided into two sub-families. The forms with the leaves opposite or in whorls are included in the *Cupressineae*; they also have the ovules erect. All the forms with alternate leaves are included in the *Abietineae*, and, almost without exception, they also possess inverted ovules.

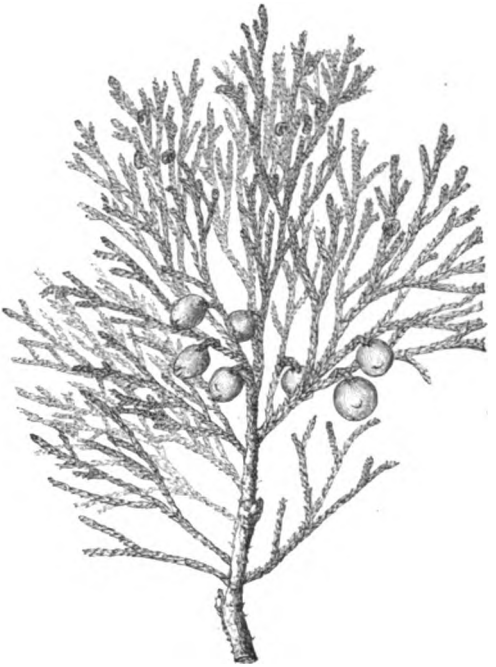


FIG. 588.—*Juniperus Sabina*: branch with fruit. *Poisonous.* (After H. SCHENCK.)

Sub-family **Cupressineae**.—Some of the Cupressineae have needle-shaped leaves in whorls (Juniper, Fig. 587); others have decussately-arranged, scale-like leaves (*Thuja*, *Juniperus sabina*, Fig. 588). The former type is to be regarded as the more primitive, for the seedlings of *Thuja* have needle-shaped leaves, and individual branches of scale-leaved forms of *Juniperus* revert to the needle-shaped leaves in whorls of three. The short shoots of *Taxodium distichum* have two ranks of leaves and are shed as a whole.

The Cupressineae, with the exception of *Juniperus*, are monoecious. The male flowers of *Juniperus communis* stand in the leaf axils. At their base are a number of small scale leaves (Fig. 587 *A*, *a*), above which come several whorls of peltate sporophylls (*c*) bearing 2-4 microsporangia (*d*) on the lower surface. The sporangia open by a vertical slit parallel to the long axis of the sporophyll. The female flowers occupy a corresponding position. The scale leaves at the base (Fig. 587 *B*) are succeeded by a whorl of carpels (*C*, *b*), each of which bears a single upright ovule

in a median position (*c*). After fertilisation a succulent parenchymatous growth mainly of the basal portions of the sporophylls raises the seeds and presses them together, without, however, obliterating the central space altogether. The three carpels become completely coherent above the seeds, but the place of union is still indicated by the scar at the apex of the ripe fruit. The succulence of the carpels gives the fruit the appearance of a berry. *Juniperus* is the only genus of the Cupressineae with such fruits; the others, such as *Cupressus*, *Thuja*, *Taxodium*, have cones, and bear the ovules on a slight outgrowth of the scale.

Juniperus communis, Juniper, is a shrub or small tree distributed over the northern hemisphere. *J. Sabina*, a prostrate shrub of the Alps and other moun-

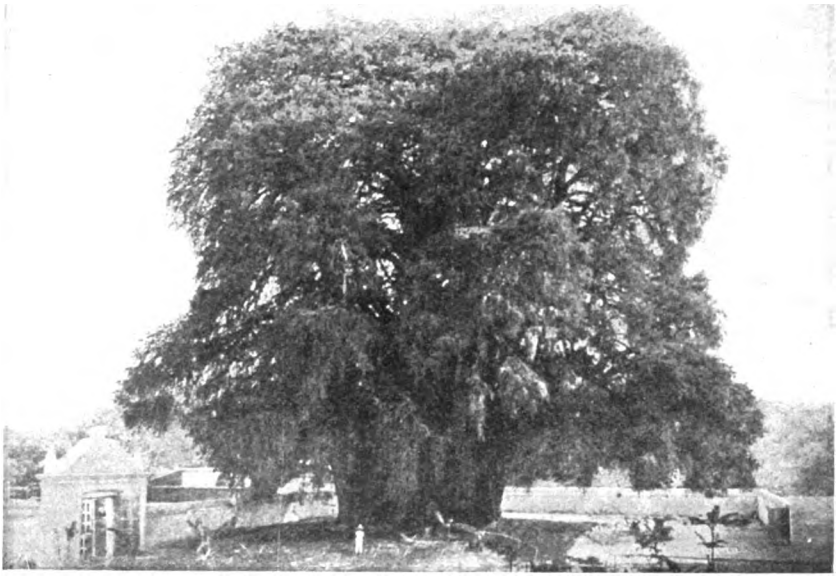


FIG. 589.—*Taxodium mexicanum* in the churchyard of S. Maria de Tule at Oaxaka. This giant tree is one of the oldest living. (From a photograph.)

tains of central and southern Europe. The Cypress (*Cupressus sempervirens*) in the Mediterranean region. Species of *Thuja* are commonly grown as ornamental trees. *Taxodium distichum* is a deciduous tree, forming extended swampy woods on the north coast of the Gulf of Mexico from Florida to Galveston. *T. mexicanum* is evergreen and is widely distributed on the highlands of Mexico; very large specimens occur such as the giant tree of Tule, which at a height of 40 m. was 30 m. in circumference, and was estimated by VON HUMBOLDT to be 4000 years old (Fig. 589).

Sub-family **Abietineae.**—The floral structure of the Abietineae may be described in the first place. The male flowers (cf. p. 544) consist of an axis bearing scale leaves at the base, and, above this, numerous stamens; the pollen-sacs (microsporangia) are situated on the lower surface of the stamen. In the Abietineae in the narrower sense there are two pollen-sacs, but in *Agathis* and *Araucaria*

there are 5-15. The microspores are usually winged. The female flowers are always cones, consisting of an axis bearing the closely approximated scales, which protect the ovules; the scales later become lignified. In *Agathis* and *Araucaria* each scale bears a single anatropous ovule at its base. The condition of affairs in *Sequoia* and *Sciadopitys* is similar, but the outgrowth is more clearly defined; each scale bears 4-9 anatropous ovules. In the Abietineae proper the limits of the two scales are still more marked. The two anatropous ovules are borne on an

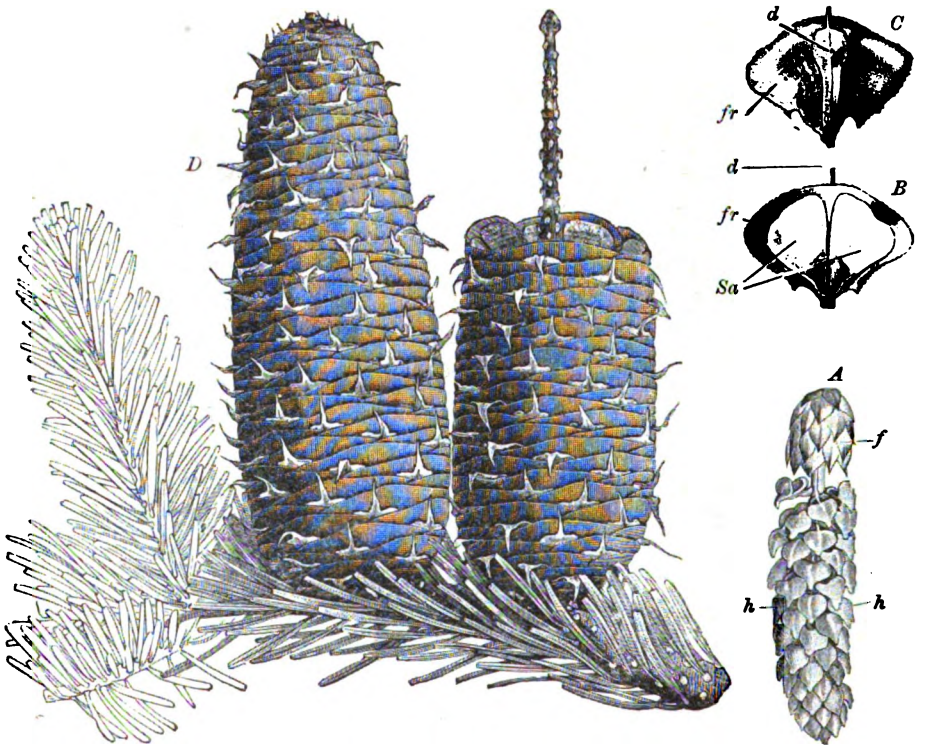


FIG. 590.—*Abies pectinata*. *A*, Male flower; *f*, scale leaves; *h*, sporophylls. *B*, Bract-scale (*d*) and ovuliferous scale (*fr*), seen from below. *C*, The same from above, *sa*, the winged seeds. (After BERG and SCHMIDT.) *D*, *Abies Nordmanniana* with ripe cones, the scales in part shed. (Reduced from ENGLER and PRANTL.)

inner scale, which, at its base, is continuous with the scale of the cone. THE OUTER SCALE IS CALLED THE BRACT SCALE, THE INNER THE OVULIFEROUS SCALE (Figs. 590, 593). The ovuliferous scale is the more strongly developed, and it is the part that becomes lignified and affords protection to the ovules. Even at the period of flowering the bract scale is usually concealed by the ovuliferous scale and only to be detected on close inspection. In other forms, however (*e.g. Abies*, Fig. 590, *Pseudotsuga Douglasii*, etc.), the bract scales even in the older cone project prominently between the ovuliferous scales.

Most important Genera and Species.—*Agathis* (*Dammara*) is distributed in the Malayan Archipelago and extends to New Zealand; *A. australis* and *A.*

Dammara yield Kauri Copal but no Dammar Resin; *Araucaria brasiliana* and *A. imbricata* are stately S. American forest trees. The genus *Sequoia* includes the most gigantic trees known; specimens of *S. gigantea* from the Californian Sierra Nevada attain a height of 100 m. and a diameter of 12 m. The beautiful *S. sempervirens* from the coastal mountains is hardly inferior in size.

The Silver Fir (*Abies pectinata*, Fig. 590 *A-C*) is a native of the mountains of the middle and south of Europe. It bears only long shoots. The flat, needle-like leaves, marked below by two white lines and emarginate at the tip, are borne on all

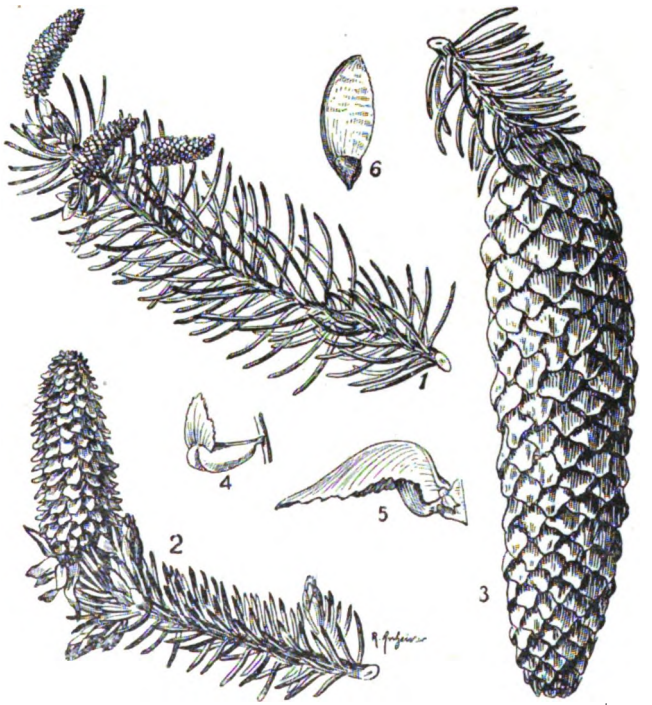


FIG. 591.—*Picea excelsa* (¼ nat. size). *1*, Twig with male flowers. *2*, Terminal female flower. *3*, Pendulous cone. *4*, Microsporophyll. *5*, Macrosporophyll: the bract-scale is covered by the large, bent-back, ovuliferous scale; an ovule is visible at the base of the ovuliferous scale. *6*, Ripe seed with the wing formed by a detached portion of the ovuliferous scale. (× 4-6.)

sides of the axis, but are twisted into a horizontal position on the branches illuminated from above. They live for 6-8 or even for 15 years. The male flowers stand in the leaf-axils on the under side or on the flanks of the shoot, and grow downwards so that the pollen-sacs are directed upwards. The wall of the sporangium opens by an obliquely longitudinal split, which gapes widely and allows the winged microspores to escape. The female flowers arise from the upper side of a branch and are directed vertically upwards. The bract-scales are longer than the broad, ovuliferous scales. The fertilised cones retain the upright position, and when ripe the scales separate from the axis and so set the seeds free from the plant. The development of the seeds takes a year. *Abies*

Nordmanniana from the Caucasus (Fig. 590 *D*), *A. concolor*, *A. balsamea*, and *A. nobilis* from N. America are in cultivation.

Picea excelsa, the Spruce (Fig. 591), is a fine tree of pyramidal shape; it has no short shoots, and the long shoots bear on all sides pointed, quadrangular, needle-shaped leaves, which on horizontal or pendulous branches stand more or less erect. They live for 5-7 years, and on main shoots for 12 years. Male flowers as a rule on shoots of the previous year; on flowering they become twisted into an erect position. The two pollen-sacs open by a longitudinal slit. Female flowers terminal on the shoots of the previous year, usually near the summit of the tree. They stand erect at the time of flowering. The ripe cones are pendulous and, after setting free the seeds from between the scales, fall in pieces. The development of the seeds is completed in one year. *Picea orientalis* from Asia Minor, *Picea omorica* from Serbia, and *Picea alba* from N. America are frequently cultivated.

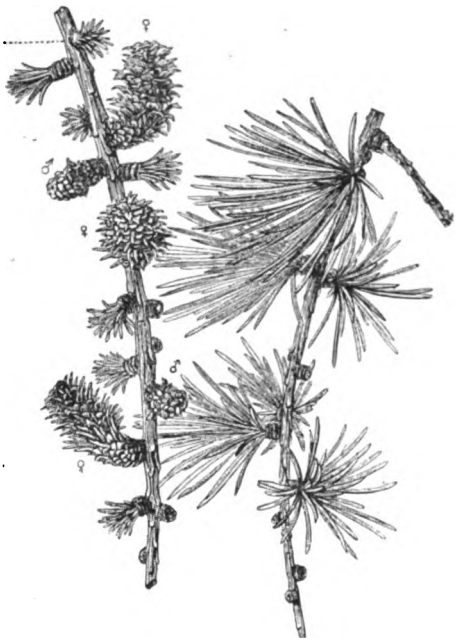


FIG. 592.—*Larix europaea*. Long shoots of the preceding year, that on the right bearing vegetative short shoots and that on the left male and female flowers in place of them. (From ENGLER and PRANTL.)

Larix europaea, the Larch (Fig. 592), is one of the few deciduous Conifers and replaces its foliage annually. There is a differentiation into long and short shoots. The former bear the narrow linear leaves on all sides and continue the branching of the pyramidal tree, the lower branches of which often droop downwards. The short shoots arise in the axils of the leaves of the long shoots of the preceding year, and bear a rosette of 30-40 leaves which are somewhat shorter but resemble those of the long shoots. The flowers occur in a position corresponding to that of the short shoots. The male flowers are bent downwards when fully developed, and the opening of the upwardly directed pollen-sacs occurs as in *Abies*. The erect female cones produce seed in the same year. Species of *Cedrus* are evergreen forest trees from the Atlas Mountains, Lebanon, and the Himalayas, and are grown in pleasure grounds.

The most advanced differentiation of the vegetative organs is found in the genus *Pinus*; *P. sylvestris*, the Scotch Fir, will serve as an example (Fig. 593). Young seedlings in the first or second year have long shoots bearing needle-shaped leaves. On older plants this type of foliage is lost; the needles are replaced by colourless, membranous scale leaves in the axils of which stand the short shoots (cf. the explanation of Fig. 593). The needles are shed in three years. The seeds ripen in the second year, and are set free by the separation of the scales of the

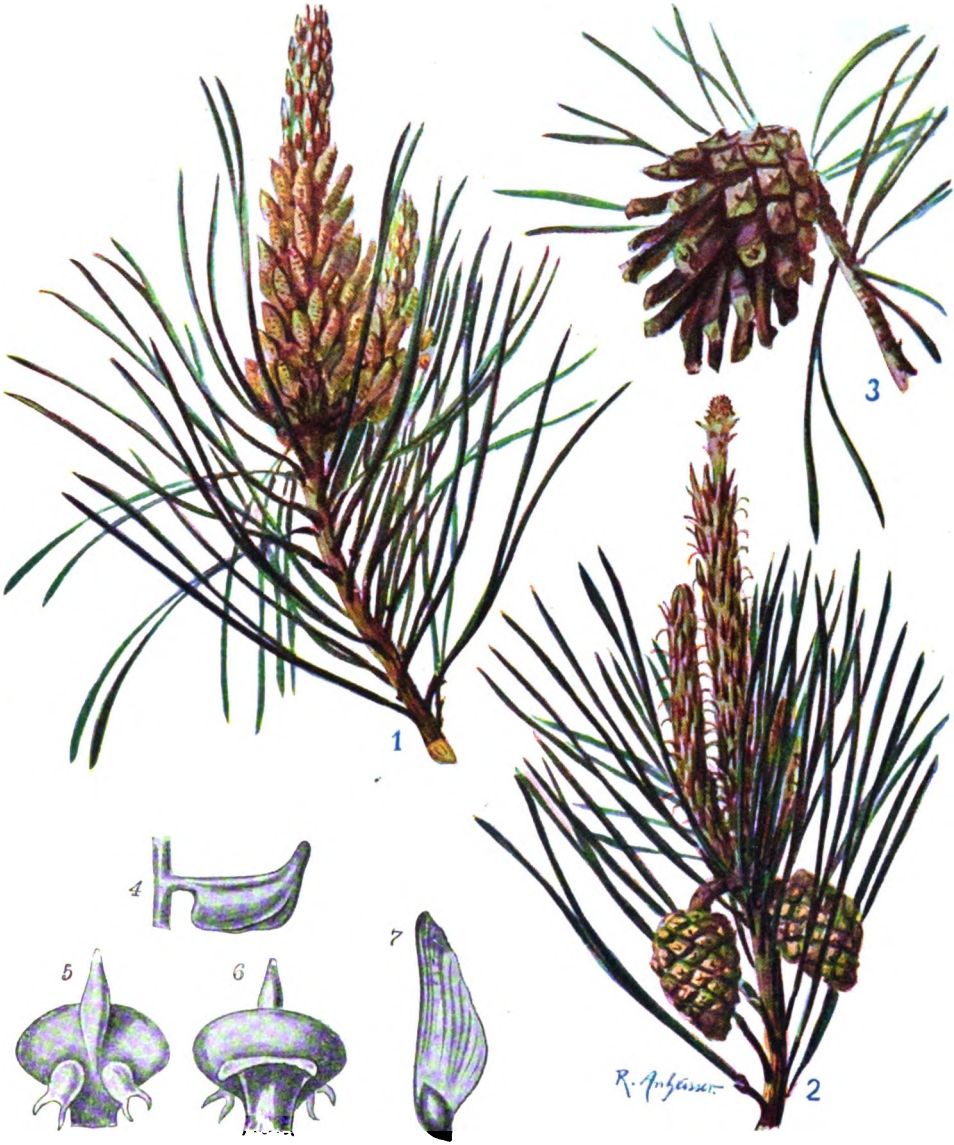


FIG. 593.—*Pinus sylvestris* (¼ nat. size). *1*, Shoot of unlimited growth bearing short shoots: at the top the shoot of the current year. At the base of the latter are numerous male flowers each in the place of a short shoot, and nearer the tip brown scale leaves, in the axil of each of which is a short shoot. *2*, Similar branch bearing a young female flower at the summit of the shoot of the current year, in place of a branch of unlimited growth. Two dependent green cones are borne on the shoot of the preceding year. *3*, Cone of the year before last, opened to allow of the escape of the seeds. *4*, A microsporophyll. *5*, Macrosporophyll from the adaxial side showing the ovuliferous scale with the two ovules at the base. *6*, Macrosporophyll from the abaxial side showing the small bract-scale below the large ovuliferous scale. *7*, Ripe seed with its wing derived from the superficial layers of the ovuliferous scale. (× 4-7.) OFFICIAL.

cone, which till then have been closely pressed together. The cones subsequently are shed. *Pinus montana*, a dwarf Pine occurring on mountains; *P. pinea*, *P. cembra*, with edible seeds; *P. laricio*, Corsican Pine from Austria; *P. Pinaster*, Maritime Pine from the Mediterranean region; *P. taeda*, *P. Strobus*, Weymouth Pine, *P. Lambertiana* from N. America.

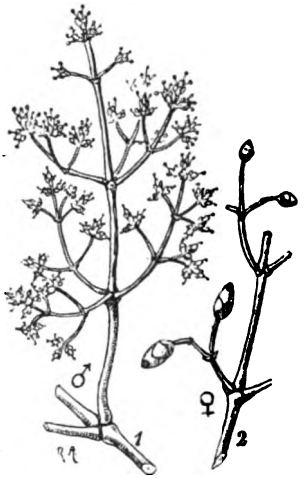


FIG. 594.—*Ephedra altissima*. *1*, Habit of a male inflorescence. *2*, An inflorescence with unripe fruits. (½ nat. size.)

POISONOUS.—*Juniperus Sabina*, *Taxus baccata*.

OFFICIAL.—*Juniperus oxycedrus* and other species yield OLEUM CADINUM; *Juniperus communis*, OLEUM JUNIPERI; *Abies balsamea* supplies TERBINTHINA CANADENSIS; *Abies sibirica* supplies OLEUM PINI SIBIRICAE; *Pinus sylvestris* and other species produce OLEUM TEREBINTHINAE and RESINA; *P. sylvestris*, etc., PIX LIQUIDA; unofficial products are obtained from other species of *Pinus*.

Order 4. Gnetinae

The only Family in this order is that of the **Gnetaceae**, to which only three genera belong: *Ephedra* (Fig. 594), leafless shrubs of warm dry regions of the northern hemisphere; *Welwitschia mirabilis* (Fig. 595), a monotypic plant from the deserts of South-West Africa; the widely expanded summit of the stem bears after the cotyledons only a single pair of leaves, which are 1 m. in length and continue to grow at their bases; *Gnetum* (Fig. 597), tropical trees or climbers with broad, reticulately-veined leaves. These

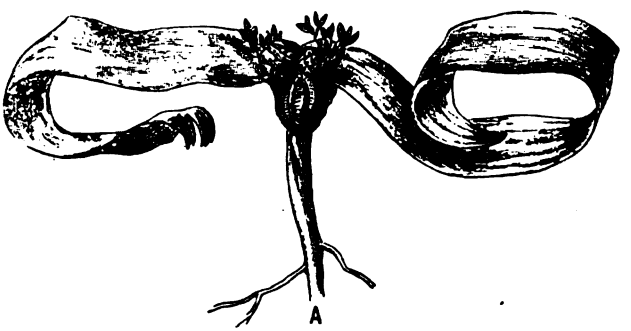


Fig. 595.—*Welwitschia mirabilis*. Young plant (from ENGLER and PRANTL).

genera, while differing widely in appearance, agree in possessing opposite leaves (in *Ephedra* reduced to scales), in the development of vessels in the secondary wood, the absence of resin canals, and in the presence of a perianth to the flowers, which are usually dioecious (Fig. 596).

These points of agreement with both Gymnosperms and Angiosperms make the group in many ways an intermediate one between the two classes. Insects visit the flowers of all three genera, though they are as yet only known to effect

pollination in the case of *Ephedra campylopoda*. On the development of the sexual generation cf. p. 569.

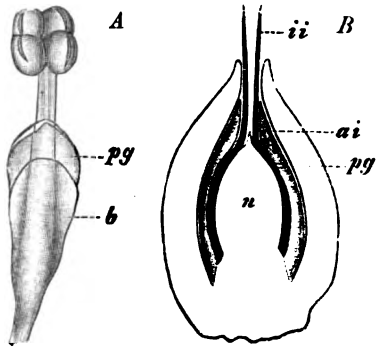


FIG. 596.—*A*, *Ephedra altissima*. Male flower (× 16, after STRASBURGER); *pg*, perigone; *b*, leaf. *B*, *Gnetum Gnemon*, longitudinal section of a female flower (× 32, after LOTSY); *n*, nucellus; *ii*, inner, and *ai*, outer integuments; *pg*, integument-like investment or perianth

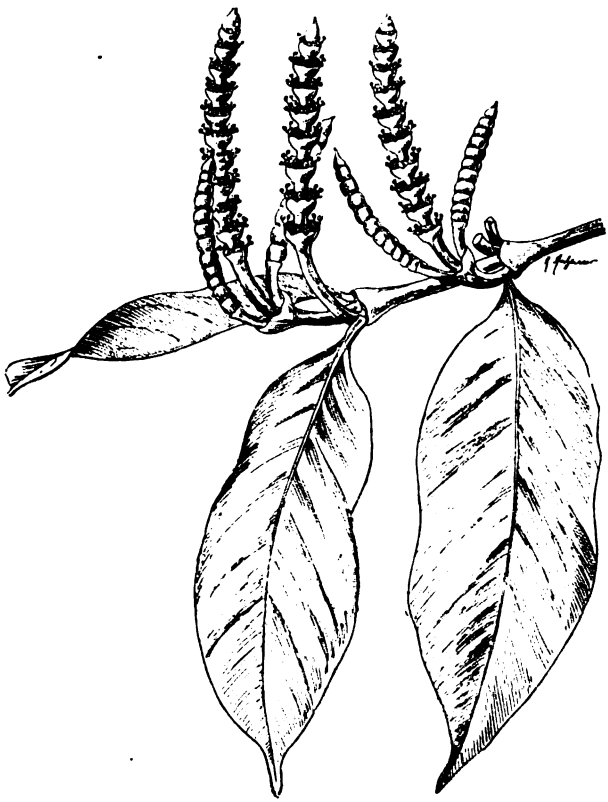


FIG. 597.—*Gnetum Gnemon*. Branch with male inflorescences. (½ nat. size.)

Fossil Gymnosperms [15]

In contrast to what was seen to be the case for the Pteridophyta, Gymnosperms have not yet been detected in Cambrian and Silurian strata. They appear first in

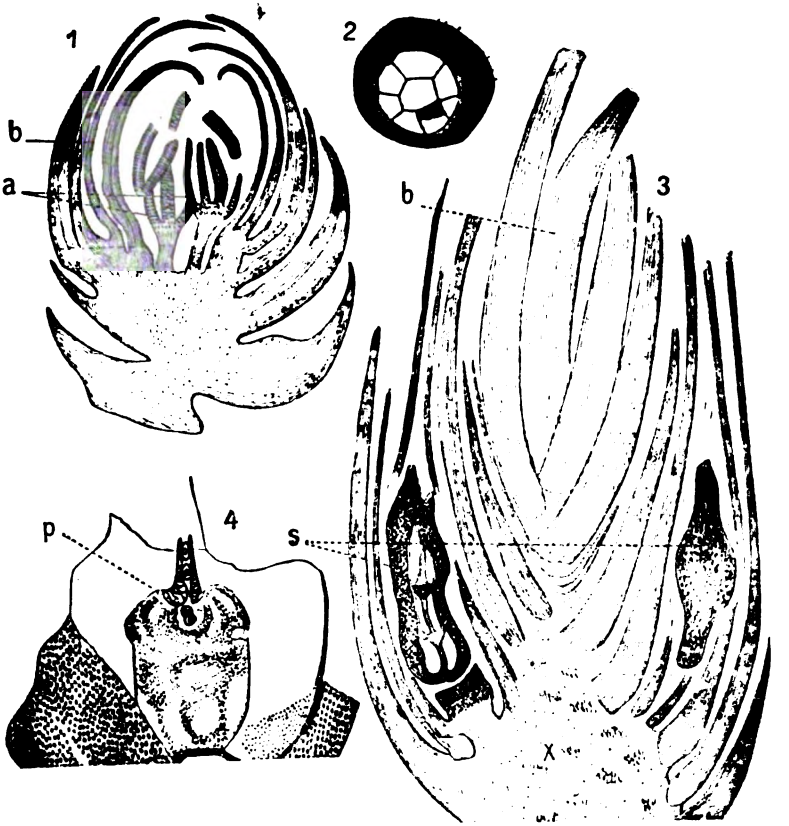


FIG. 598.—*1*, *Cordaites subglomeratus*, longitudinal section of a male flower-bud; *b*, investing bracts; *a*, stamens with several anthers. *2*, A pollen grain; the prothallial cell is separated by a curved wall while the rest of the grain is divided into a number of cells. *3*, *C. Williamsoni*, longitudinal section of a female inflorescence; *b*, leaves; *s*, seed in longitudinal section. *4*, *C. Grand'Euryi*, longitudinal section of an ovule, showing the deep pollen chamber in the nucellus containing a number of pollen grains. (After RENAULT.)

the Devonian, but are sparingly represented and first form an important constituent of the flora in the Carboniferous. From the **Cycadofilices**, which possessed stems with secondary thickening and fern-like foliage and had been regarded as Pteridophyta, OLIVER and SCOTT have recently separated the **Pteridospermeae**; which may be shortly characterised as fern-like seed-plants. These have been considered in connection with the Pteridophyta (p. 534).

Cordaitaceae.—*Cordaites* is a peculiar type confined to the Palaeozoic rocks. Owing to the excellence of the preservation of the remains, its morphology is as

well known as that of the existing Gymnosperms. The Cordaitaceae were lofty, branched trees with linear or broad and lobed leaves with parallel venation. Their flowers differ considerably from those of recent Gymnosperms. The male and female flowers are borne on spike-like axillary inflorescences. The female flower consists of a single atropous ovule with some bracteoles at its base; these resemble the vegetative foliage leaves (Fig. 598, 3, 4). At the summit of the nucellus is a deeply sunken pollen chamber in which pollen grains are often met with. The male flowers terminate small shoots that are surrounded by a number of sterile bracts and at the summit produce a number of stamens each of which has 2-4 anthers (Fig. 598, 1). An important fact as bearing on the phylogeny of the group is the presence of a male prothallus as a small

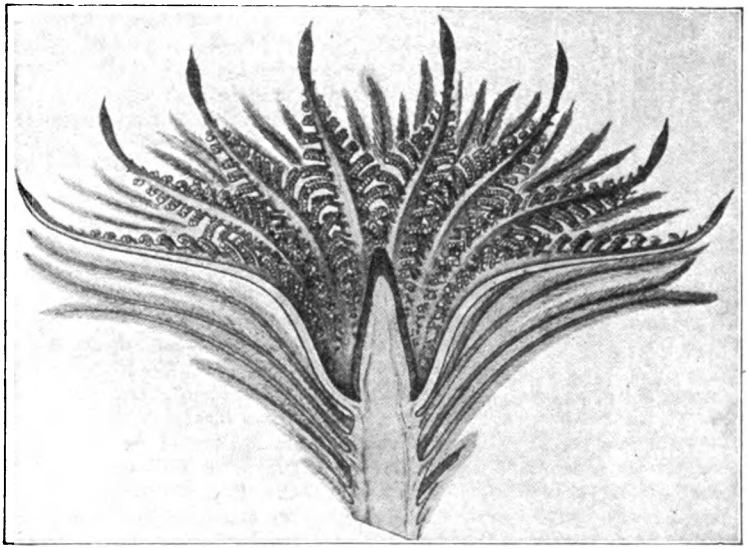


FIG. 599.—Reconstruction of the longitudinal section of the flower of *Cycadeoidea* (*Bennettites*) *ingens*. (From SCOTT after WIELAND.)

multicellular body (Fig. 598, 2). The ovules and seeds show great structural agreement with those of *Cycas* and *Ginkgo*. With the exception of some less common fossils (*Cycadites*, *Dicranophyllum*), which may be placed with the Ginkgoineae, *Cordaites* is the most richly represented type of Gymnosperm found in the Carboniferous rocks. Undoubted Cycadophyta make their appearance in the lower Rothliegende.

The Cordaiteae disappear in the lower Mesozoic strata. The Gymnosperms flora can be followed through the Trias, in which it consisted of extinct types of Cycadophyta, Ginkgoineae, and Coniferae, to the Jurassic period. In the latter it attained a great development in that both the Ginkgoineae and the Cycadophyta attained their maximum development.

Bennettitaceae.—SCOTT has recently given an account of the appearance and the high degree of organisation attained by the Mesozoic Cycadophyta, from the knowledge obtained by WIELAND'S study of the abundant material found in North America. The name *Cycadeoidea* proposed by the American author is synony-

mous with *Bennettites*; fruits derived from the hermaphrodite flowers were already imperfectly known from European strata under the latter name. The short and sometimes branched stems resembled recent Cycads in their appearance and foliage and bore flowers which were hermaphrodite and 12 cm. in length. A hundred or more spirally arranged perianth leaves surrounded a whorl of 18-20 microsporophylls, which were united at the base to form a deep cup, in the centre of which the gynaeceum arose (Fig. 599). The pinnate microsporophylls, 10 cm. in length, resemble the leaves of Ferns, and the microsporangia resemble the sporangia of the Marattiaceae. The gynaeceum consists of numerous, long-stalked, atropous ovules which are surrounded and separated by scale leaves: the microsporophylls, however, open freely on the exterior. The ripe seeds contained a highly developed dicotyledonous embryo and had no endosperm. They were protected and enclosed by the closely crowded outer ends of the scale leaves (Fig. 600). Just as the Palaeozoic Pteridosperms combine the characters of Ferns and Gymnosperms, the flowers of the Mesozoic *Bennettites* or *Cycadeoidea* show a combination of characters of Angiosperms, Gymnosperms, and Ferns.

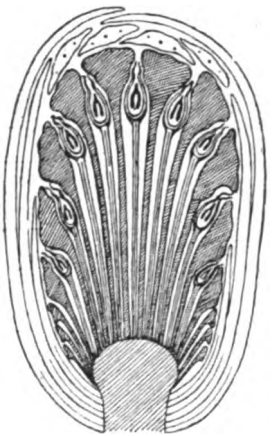


FIG. 600. — Longitudinal section of a fruit of *Bennettites Gibsonianus*. (After SCOTT.)

True Araucarieae appear in the Jurassic; on this account, as well as on account of their organisation, this group may be regarded as the oldest of the existing Coniferae. In the Wealden, Cycadineae and Ginkgoineae along with some Coniferae were dominant among the Gymnosperms. On passing to the Cretaceous strata the ancient types are found to be reduced, while the Coniferae become more numerous. Among the latter appear existing genera (*Dammara*, *Sequoia*, *Pinus*, *Cedrus*, *Abies*, *Callitris*, etc.). The Taxaceae also appear to be represented, but the remains are of uncertain affinity.

The Tertiary Gymnosperms belong entirely to existing types and for the most part to existing species. The Coniferae are dominant; the Ginkgoineae are represented only by *Ginkgo biloba*, but this occurred in Europe along with other species now limited to Eastern Asia or North America (*Cryptomeria japonica*, *Taxodium distichum*, *Sequoia gigantea*, *S. sempervirens*, *Pinus Strobus*, etc.). One Cycadaceous plant (*Encephalartos*) is also known.

CLASS II

Angiospermae [16]

The long-disputed question as to whether the Monocotyledons or Dicotyledons are the more primitive is perhaps settled by the derivation of the Monocotyledons from the Polycarpicae among the Dicotyledons; these exhibit features of agreement with Monocotyledons in floral construction, anatomical structure, and in morphological characters. On this account the Monocotyledons will be placed after the Dicotyledons in the following systematic arrangement.

Any direct transition from Gymnosperms to Monocotyledons is thus out of the question while a relation of dicotyledonous plants to Gymnosperms is not excluded. The parallels and progressive developments that can be recognised in the male and female organs have been referred to above (p. 544 f.); there are also indications of the derivation of the one group from the other in the construction of the flower as a whole. In attacking this problem WETTSTEIN attempts to derive the simplest flowers of the Angiosperms from Gymnosperm inflorescences.

A male flower with a single perianth and superposed stamens could be derived from a whorl of scale leaves with simple axillary male flowers. Since in male inflorescences of *Ephedra* single female flowers occasionally appear, it is possible that the female organs might become associated with the stamens. The probability of such a transition is increased by the fact that insect-pollination has been observed in inflorescences of this kind.

If the systematic arrangement of the Dicotyledons is based on this idea, the most simply constructed flowers would be those with one whorl of perianth segments and borne in catkins. Thus the Casuarinaceae, Juglandaceae, Betulaceae, Ulmaceae, etc., will be placed at the beginning of the system, and to them will be connected the other families with a simple perianth which are grouped together as Monochlamydeae. To these in turn may be connected the Dialypetalae, the flowers of which have both calyx and corolla. The forms with a gamopetalous corolla are separated as the Sympetalae, and the other Monochlamydeae and Dialypetalae contrasted with them as Choripetalae; the forms without perianth are grouped with the Choripetalae. Since within the Monochlamydeae various lines lead from forms with a simple perianth to those with a pentacyclic structure, any arrangement in a simple ascending series is impossible. Various parallel series lead from simple to highly organised floral structure, and similarly numerous parallel series are found in the Dialypetalae. Thus the natural or phylogenetic relationships can only be exhibited in an incomplete fashion in the following arrangement.

In addition to this line of transition from Gymnosperms to Angiosperms another possibility has to be seriously considered; this was pointed out a considerable time ago by H. HALLIER. He treated the Polycarpicae, from which the Monocotyledons have been derived above, as the starting-point for the Dicotyledons generally. This view finds support in a biological observation of DIELS ([17]), who showed that both some South African species of *Encephalartos* and some of the Polycarpicae are pollinated by beetles. Since the Coleoptera are the phylogenetically oldest flower-visiting insects and appear as the pollinating agents in the oldest family of Gymnosperms, a similar age may be inferred for the Polycarpicae that are pollinated by beetles.

The morphological construction of the flower of the Polycarpicae, with its spiral arrangement of all the floral leaves, presents resemblances to the greatly

elongated axis of the flowers of Gymnosperms. The Gnetaceae, which are also treated by WETTSTEIN as a connecting link between Gymnosperms and Angiosperms, foreshadow in the androgynous inflorescence of *Gnetum* a flower like those of the Polycarpicae. Further, the Calycanthaceae, which are placed in the latter group, have an extensive sporogenous tissue in the nucellus such as is only known in some Gymnosperms, in *Casuarina*, and in Rosaceae, a family that is to be connected with the Calycanthaceae.

The evidence for this second possible line of progression renders it as probable as the one first mentioned. Both regard the Gnetaceae as a transition family, and it is thus conceivable that both lines of development have been followed in plant-evolution. The less highly organised Monochlamydeae would come in the manner indicated by WETTSTEIN from *Ephedra* to Dicotyledons; the Dialypetalae in the second way from *Gnetum* to the Polycarpicae. So long as developmental and morphological evidence is insufficient to establish a common origin of the two sets of Dicotyledons and their connection as suggested by HALLIER in the Hamamelideae, this double origin appears most probable.

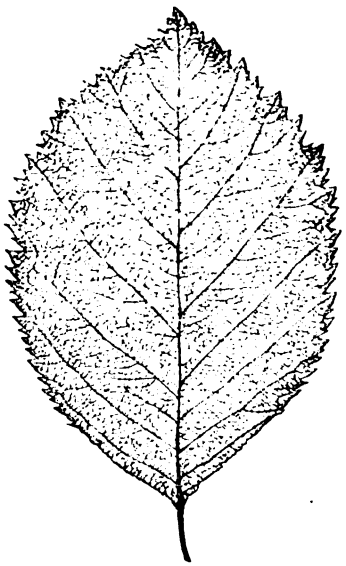


FIG. 601.—Leaf of *Crataegus* with reticulate venation. (⅔ nat. size. After NOLL.)

SUB-CLASS I

Dicotylae

The Dicotyledons with few exceptions possess a pair of seed-leaves. The distinction of hypogeal and epigeal germination has been described on p. 589.

The stem has a circle of open vascular bundles, while the root on transverse section shows a regularly alternating arrangement of the xylem- and phloem-groups (cf. p. 136, Fig. 163). The meristem situated in the vascular bundles of the stem, or to the inner side of the phloem in the root, soon becomes completed across the medullary rays and forms a complete, meristematic ring. By means of this cambium a regular growth in thickness of the stem and root takes place.

The typical form of leaf found among Dicotyledons is provided with a longer or shorter petiole, and often has a pair of stipules developed from the leaf-base; a leaf-sheath is usually absent. The lamina may be simple or compound; the latter condition is always

the result of lateral branching during the development of the leaf. The margin of the leaf presents considerable variety. The venation is as a rule reticulate (Fig. 601).

The flowers in Dicotyledons are typically pentamerous and pentacyclic, but there are numerous exceptions to this. The floral formula in the most regularly constructed representatives is K5, C5, A5 + 5, G5.

Series I. Choripetalae

A. Monochlamydeae

The following orders 1-4 agree in the unisexuality and anemophily of their flowers with simple uncoloured perianth. They include various transitional forms from chalazogamy to porogamy.

Order 1. Juglandiflorae

Family **Juglandaceae.**—Conspicuous, monoecious trees of the northern hemisphere with imparipinnate, aromatic leaves arranged alternately. Stipules wanting.

The Walnut, *Juglans regia* (Fig. 602), is the best-known representative of the family. It is endemic in Western Asia and the eastern portion of the Mediterranean region, but the tree is in cultivation throughout Europe. In spring the axillary buds of the previous season produce long, thick, pendulous catkins bearing numerous flowers. Each of the latter has 3-5 perianth segments, and these together with the two bracteoles are adherent to the bract and surround the numerous stamens, which face towards the tip of the inflorescence. The female flowers in smaller numbers are borne at the summit of the young shoots. The two carpels terminate in large, feathery, diverging stigmas. The perigone is adherent to the bract and bracteoles and reaches to the summit of the inferior ovary. The single loculus encloses an atropous, basal ovule. Fruit, a drupe. The exocarp contains abundant tannin. The hard endocarp is divided into two valves in the plane of the dorsal sutures of the coherent carpels, the limits of which are indicated by the partial septum at the lower part of the fruit. Within the stone is the embryo, enclosed in a thin seed-coat. The large cotyledons, which contain oil, are lobed in correspondence with the false septa that project from the inner surface of the ovary. Endosperm wanting. Other species of *Juglans* and *Carya* yield edible seeds and valuable timbers.

Order 2. Quercifiorae ([18])

Trees or shrubs usually with entire leaves and deciduous stipules. Monoecious. Flowers in catkins. Ovary inferior; ovules pendulous. Fruit, a one-seeded nut. Endosperm wanting. Anemophilous. This order includes most of our important forest-trees.

Family 1. **Betulaceae.**—Male flowers adherent to the bracts. Ovary bilocular, with two long stigmas; a single, pendulous ovule in each loculus. Mainly distributed in the northern hemisphere.

MOST IMPORTANT GENERA.—*Alnus glutinosa*, the Alder, is a prominent tree of damp woods, and is also distributed in swamps and by the banks of streams. The inflorescences are already evident in the autumn as stalked catkins, the male long and pendulous, the female erect and short. Male flowers P4, A4 ; a dichasium of three flowers adherent to each bract (Fig. 603). The female flowers are in

FIG. 602.—*Juglans regia*. *1*, Branch with young leaves, male catkins and at the tip female flowers. *2*, Male flower. *3*, Female flower. *4*, Fruit with the outer layer of the pericarp in part removed. (½ nat. size.)

pairs, their bracteoles adhering to the bract to form the five-lobed, persistent, woody scale of the cone. *Alnus incana* is distinguished by its leaves being grey and hairy below. *Betula verrucosa* (Fig. 604), the Birch, has a white bark and long stalked, triangular leaves. When young, all the parts are covered with numerous glandular hairs which give the plant an aromatic, resinous odour. The male inflorescences are formed in the autumn of the previous year, singly or a few together, at the tip of shoots of unlimited growth. Flowers P2, A2; in dichasia

of three, adherent to the bract. Anthers deeply bifid (Fig. 604, 3, 4). Female inflorescences solitary, at the apex of small, short shoots of the current year. Flowers in dichasia of three in relation to each three-lobed scale; the latter is composed of the bract and the two adherent bracteoles. Fruits borne on pendulous catkins; winged. After the fruits are shed the scales of the catkin separate. *Carpinus Betulus*, the Hornbeam (Fig. 605), is an important forest-tree. The inflorescences appear in spring, the male, from axillary buds of the previous year, either want leaves or are accompanied by one or two, the female are usually terminal. The bract of the male catkin bears 4-10 stamens, bifid to the base, but without bracteoles or perigone. Two female flowers in relation to each bract; each flower with its special bract and pair of bracteoles. The three latter unite to form a three-lobed involucre which serves as an aid to distribution of the fruit by the wind. *Corylus*

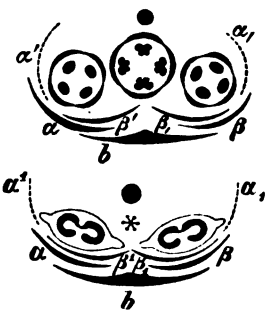


FIG. 603.—*Alnus glutinosa*. Diagrams of the male and female flowers. Bract *b*; bracteoles α β, α' β', α, β₁. (After EICHLER.)

FIG. 604.—*Betula verrucosa*. *1*, Branch with terminal male catkins and female catkins on small lateral branches. *2*, Female flower. *3*, Male flower. *4*, Stamen. *5*, A catkin in fruit. *6*, Fruit. (*1* and *5*, ⅓ nat. size; *2-4* and *6*, enlarged.)

avellana, the Hazel, develops its inflorescences in the preceding year. The male catkins are freely exposed during the winter, while the female remain enclosed by the bud-scales, and only protrude their long red stigmas between the scales at the actual time of flowering. The male flower has no perianth but has a pair of bracteoles which are adherent to the bract, as are the four deeply bifid stamens. In the short female catkins a two-flowered dichasium is present in the axil of each bract as in *Carpinus*; the fringed involucre also is derived from the coherent bracteoles and special bract of each flower. *Corylus tubulosa* from southern Europe.

Family 2. **Cupuliferae.**—Inflorescences in the leaf axils, bearing male flowers provided with a perianth, and female flowers one or

more of which are enclosed in a cupule (Fig. 606 *cp*) derived from united bracteoles. The trilocular ovary has two pendulous anatropous ovules in each chamber and ends in three stigmas.

Distributed chiefly in the temperate zones of the northern hemisphere, also in tropical Asia.

FIG. 605.—*Carpinus betulus*. *1*, Branch with male catkins projecting from the buds of the preceding year and female catkins on the growth of the current year. *2*, Female catkin in fruit. *3*, Male flower. *4*, Stamen. *5*, Bract with two female flowers. *6*, Female flower. *7*, Fruit. (*1*, *2*, *7*, ½ nat. size; *3-6* enlarged.)

MORE IMPORTANT SPECIES.—*Fagus sylvatica*, the Beech (Fig. 607), is one of our most important deciduous trees. The leaf is entire, elliptical, shortly stalked, and, especially when young, covered with fine hairs. Leaves two-ranked. Inflorescences on shoots of the current season. Male inflorescences capitate and pendulous, flowers with an oblique, bell-shaped perianth and usually 8-12 stamens. Female inflorescences terminal, capitate and erect; flowers in two-flowered dichasia. The cupule surrounds both flowers (Fig. 608 *B*), and completely envelops the triangular, nut-like fruits; at maturity it opens by splitting into four valves. Its surface is covered with numerous, blunt prickles.

Castanea vulgaris, the edible Chestnut, is a native of the Mediterranean region.

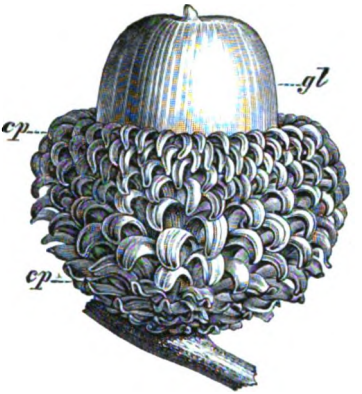


FIG. 606.—Cupule of *Quercus Aegilops*. *cp*, cupula; *gl*, fruit.
(After DUCHARTRE.)

FIG. 607.—*Fagus sylvatica*. (½ nat. size.) *1*, Branch with male and female inflorescences. *2*, Male flower. *3*, Female flower. *4*, Open cupule with two fruits. *5*, Fruit. *6*, Transverse section of a fruit showing the folded cotyledons of the embryo. (*2*, *3*, *6*, enlarged.)

The inflorescences on shoots of the current year bear in some cases only male flowers, in others female flowers at the base and male flowers above. Flowers

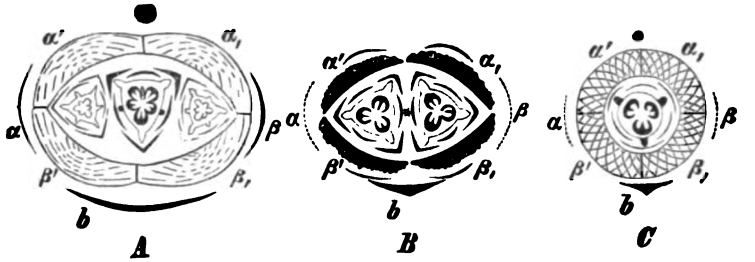


FIG. 608.—Diagrams of the female dichasia of: *A*, *Castanea vulgaris*; *B*, *Fagus sylvatica*; *C*, diagram of the single flower of *Quercus pedunculata*. *b*, Bract; *α β*, bracteoles; *α, β,, α' β'*, bracteoles of the secondary flowers adherent to the cupule. (After EICHLER.)

grouped in dichasia. Female dichasia three-flowered (Fig. 608 *A*), so that three nuts come to be enclosed within the spiny cupule, which splits into four valves. The Oaks, *Quercus pedunculata* (Figs. 609, 610) and *Quercus sessiliflora*, are the largest deciduous trees of European woods. Leaves oval, margins sinuately lobed. The pendulous male inflorescences spring, at the time that the new foliage is expanding, from axillary buds of the shoot of the preceding year or from the lowest buds of the shoot of the current year; flowers solitary, consisting of a perianth of 5-7 segments and 6-12 short stamens. Female inflorescences erect, few-flowered, in the axils of the upper leaves of the shoot of the current year. Flowers solitary; in *Q. pedunculata* with long stalks, in *Q. sessiliflora* sessile. Each flower is invested by a cupule (Fig. 608 *C*), which is at first inconspicuous, but is fully developed on the ripe fruit.

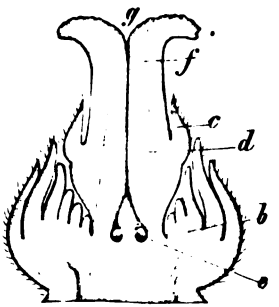


FIG. 609.—*Quercus pedunculata*, longitudinal section of the female flower. *b*, The young cupule; *e*, ovule; *d*, ovary; *c*, perigone; *f*, style; *g*, stigma. (After BERG and SCHMIDT, magnified.)

The Beech yields firewood, tar, and pyroligneous acid; the Oak provides a valuable timber, a bark containing tannin used in tanning, and cork from the Cork-oak.

OFFICIAL.—The GALLS produced on the young twigs of *Quercus infectoria* as a result of puncture by the Gall-wasp, *Cynips tinctoria*; Tannic Acid is obtained from these.

Order 3. Salicifloræ

Family **Salicaceæ**.—Trees and shrubs with simple, alternate, stipulate leaves. Flowers in dioecious catkins, usually developed before the leaves. Both male and female flowers are naked and stand in the axils of bracts. More or less developed scale-like development of the disc or floral receptacle. Ovary of two carpels, unilocular. Fruit, a capsule containing numerous, parietal seeds. Seeds without endosperm; seed-coat with a tuft of hairs.

This family is mainly represented in the north temperate zone. *Salix*, Willow, and *Populus*, Poplar, are the only genera. *Salix* has erect catkins and is adapted for pollination by insects; in relation to this, nectar is secreted by small scales at the base of the flower. Male flowers scented; pollen sticky. The number of stamens varies from 2 to 5 in the different species. Bracts entire (Fig. 611). Willows occur commonly by the banks of streams. Some species are among the

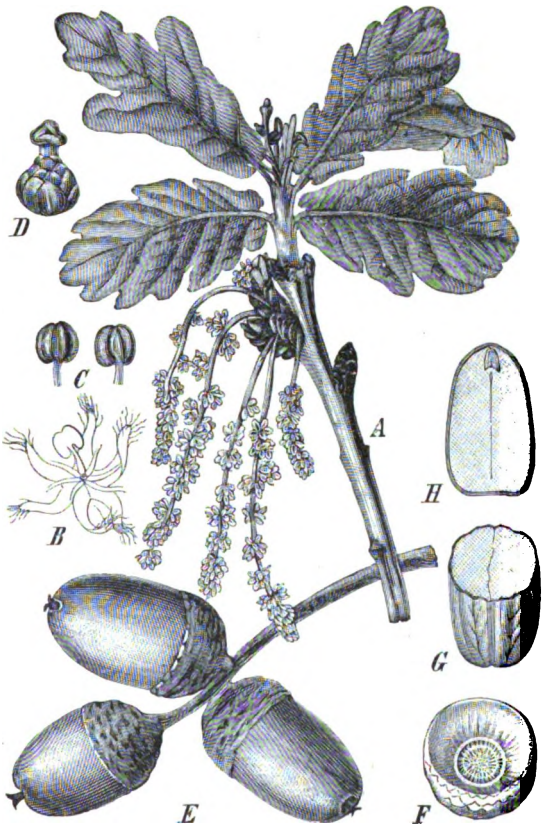


FIG. 610.—*Quercus pedunculata*. *A*, Flowering branch; *B*, a male flower (magnified); *C*, stamens (magnified); *D*, a female flower (magnified); *E*, infructescence; *F*, cupule; *G-H*, seed. (After SCHIMPER.)

more abundant plants of high northern latitudes; they have subterranean, creeping stems, only the young shoots projecting from the soil. *Populus* has anemophilous flowers; disc cup-shaped; no secretion of nectar. The long-stalked roundish leaves of the Poplars give them a different habit from the Willows. Flowers similar to those of *Salix* but with divided bracts. Catkins pendulous (Fig. 612).

SALICIN is obtained from the bark of species of *Salix* and *Populus*.

Order 4. Urticinae

Herbaceous or woody plants with small, inconspicuous flowers closely aggregated in the inflorescence. Stamens equal in number to the leaves of the perigone and superposed on the latter. Ovary superior, composed of one or two carpels, usually unilocular, and containing a single, pendulous ovule. Fruit, a nut or drupe. Seeds usually containing endosperm.

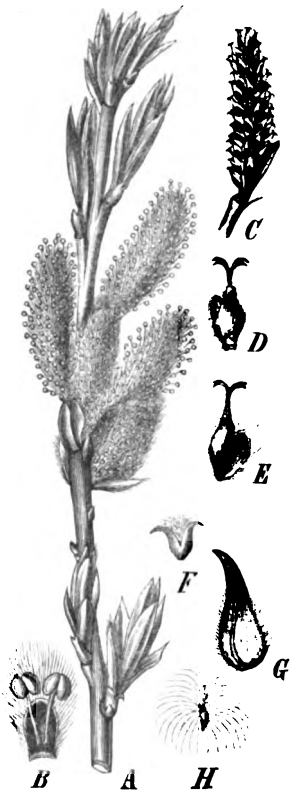


FIG. 611.—*Salix viminalis*. *A*, Flowering male twig (nat. size). *B*, Male flower with subtending bract (magnified). *C*, Female inflorescence. *D-E*, Female flowers (magnified). *F*, Fruit (nat. size). *G*, The same magnified. *H*, Seed (magnified). (After SCHIMPER.)

Family 1. **Ulmaceae.**—*Ulmus campestris* (Fig. 613), the Elm, is a common European tree. The arrangement of the leaves on the sides of the twigs in two rows and the corresponding branching leads to the leaf surface exposed on each lateral branch making a definite angle with the main branch and composing the regular convex crown of foliage exhibited by older

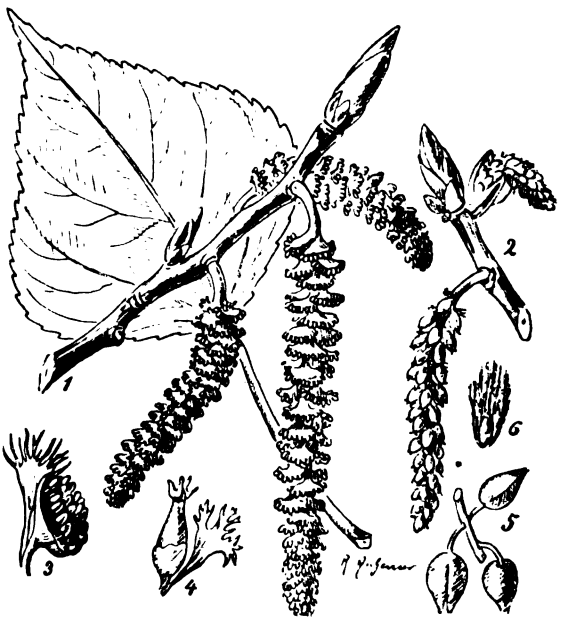


FIG. 612.—*Populus nigra*. *1*, Male inflorescence. *2*, Female inflorescence. *3*, Male flower. *4*, Female flower. *5*, Fruit. *6*, Seed. (*1*, *2*, ⅓ nat. size; *3-6*, enlarged.)

examples. The leaves are always asymmetrical. The flowers stand in groups in the axils of the leaves of the previous year; they are hermaphrodite or, by abortion, unisexual. The stamens are straight in the bud. The tree flowers in February or March and the fruits ripen before the leaves expand. The fruits

are broadly winged and adapted to be carried by the wind. *U. montana*, *U. effusa* are closely related forms. Several species of *Celtis*, in which the fruit is a drupe, are in cultivation.

Family 2. **Moraceae.**—The majority are trees or shrubs with

FIG. 613.—*Ulmus campestris* (⅓ nat. size). *1*, Branch with flowers. *2*, Branch with fruits. *3*, Single flower, enlarged.

abundant latex. Leaves alternate, stipules caducous. Flowers unisexual in globular or disc-shaped inflorescences; mostly tetramerous.

IMPORTANT REPRESENTATIVES.—In addition to the Mulberry trees, of which *Morus alba* is cultivated for the rearing of Silk-worms and *M. nigra* (Fig. 574 *B*) as a fruit-tree, the genus *Ficus* deserves special mention. The species occurring farthest north is the Common Fig (19) (*Ficus carica*, Fig. 614), which is endemic to the Mediterranean region, and has been long cultivated. It is a low tree with palmately incised leaves and stipules, which form a cap-like protection to the bud.

The inflorescences are hollow, pitcher-shaped structures with a narrow opening. The flowers are borne closely crowded together on the inner surface. The flat, disc-shaped inflorescences of *Dorstenia* which bear the flowers on the upper surface are in many respects corresponding structures. On the distribution of the fruitlets cf. GOEBEL (19). On the pollination of the Fig cf. p. 556. The sweet, fleshy portion of the edible Fig is developed from the hollowed axis of the inflorescence together with the perigones of the individual flowers. The small, hard, seed-like bodies are the fruits developed from the ovaries of the small flowers. Some species of *Ficus* are among the largest trees of tropical forests. The most remarkable is the Banyan (*Ficus bengalensis*), which occurs in the East Indies. The seeds, carried by fruit-eating birds, germinate on the branches of trees, where the plant develops as an epiphyte. The proper form of the tree is only seen, however, after the roots have reached the soil, and it is no longer dependent on the scanty food supply obtainable in the epiphytic position. The host-plant is gradually strangled, additional roots are sent down to the soil and thicken into pillar-like supports, and ultimately a small wood capable of sheltering an entire village is developed from the single small seedling. The latex of *Ficus elastica* is obtained from the tree by making incisions in the bark, and serves as one source of india-rubber. *Castilloa elastica* is another important rubber-tree of Central America. The gigantic inflorescences of species of *Artocarpus* when in fruit are eaten raw or cooked and form the Bread-fruit of the tropics.

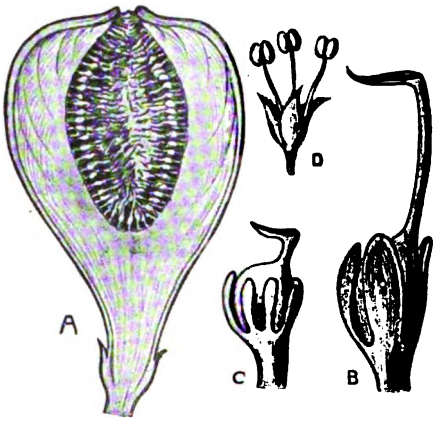


FIG. 614.—*Ficus carica*. *A*, Longitudinal section of an inflorescence. *B*, Fertile flower. *C*, Gall-flower. *D*, Male flower. (*B-D*, enlarged; *D*, after KERNER; *B*, *C*, after SOLMS-LAUBACH.) *OFFICIAL.*

OFFICIAL.—The fruits of *Ficus carica*.

Family 3. **Cannabinaceae.**—*Humulus lupulus*, the Hop, is a native of central Europe; it has a perennial rhizome, which annually produces a crop of twining shoots (Fig. 615). The stem and opposite leaves bear coarse hairs, and the former bears hooked prickles which prevent it slipping down the support. The male flowers of this dioecious plant are pentamerous, with straight stamens and grouped in dichasia the central branches of which are capable of further growth. The branches of the female inflorescence are catkin-like, the scales being formed of the pairs of stipules belonging to bracts, the laminae of which are suppressed. The axillary shoot of the bract is also suppressed, but each stipule has two flowers in its axil; each flower is enclosed by its own bract. These bracts project beyond the stipules when the inflorescence is mature, and give the latter its cone-like appearance. Upon them are developed the glandular hairs on account of which the Hop is cultivated.

Cannabis sativa, Indian Hemp, is an annual herb with palmately divided, hairy leaves, which are opposite below and alternate in the upper portion of the shoot. The female inflorescence resembles that of the Hop, but the central shoot, which

in that plant is suppressed, grows out in the Hemp to a leafy shoot. Only a single flower is present in the axil of each bract. The same process is repeated in the axil of each leaf of the leafy middle shoot, so that the whole female inflorescence is a repeatedly branched structure. The plant is utilised in Europe for its bast fibres, which are from one to several centimetres long. The glandular hairs which cover all parts of the female inflorescence secrete a sticky resinous substance

FIG. 615.—*Humulus lupulus*. *1*, Male inflorescence. *2*, Female inflorescence. *3*, Two female flowers in the axil of a bract. *4*, Cone-like inflorescences in fruit. (½ nat. size.)

which is used medicinally. In the East it is used in the preparation of a narcotic called Haschisch.

OFFICIAL.—*Cannabis sativa* provides CANNABIS INDICA.

Family 4. **Urticaceae.**—Perennial herbs or less commonly shrubs. Leaves simple, stipulate. Flowers unisexual by suppression of parts, as a rule bimerous. P 2+2, A 2+2. Stamens inflexed in the bud, and scattering the pollen when they suddenly straighten. Ovary consisting of a single carpel, unilocular, with a basal, atropous ovule. Perianth of the female flower adherent. Flowers in dichasia, or crowded in dorsiventral inflorescences. Anemophilous. Widely spread in the tropics.

A number of the Urticaceae are characterised by the possession of stinging hairs (cf. Fig. 55), *e.g.* the common Stinging Nettles, *Urtica dioica* and *U. urens*, and the dangerous tropical species of *Laportea*. Some provide important fibres, especially *Boehmeria nivea* from which Ramie fibre is obtained, and of less value, *Urtica cannabina*, and our native species of *Urtica*.

Orders 5-7 are isolated, and also have no evident connection with one another.

Order 5. Loranthiflorae

Family 1. **Santalaceae.**—Green plants growing in the soil and partially parasitic on the roots of other plants from which their haustoria obtain nutrient materials. In Britain, *Thesium.*

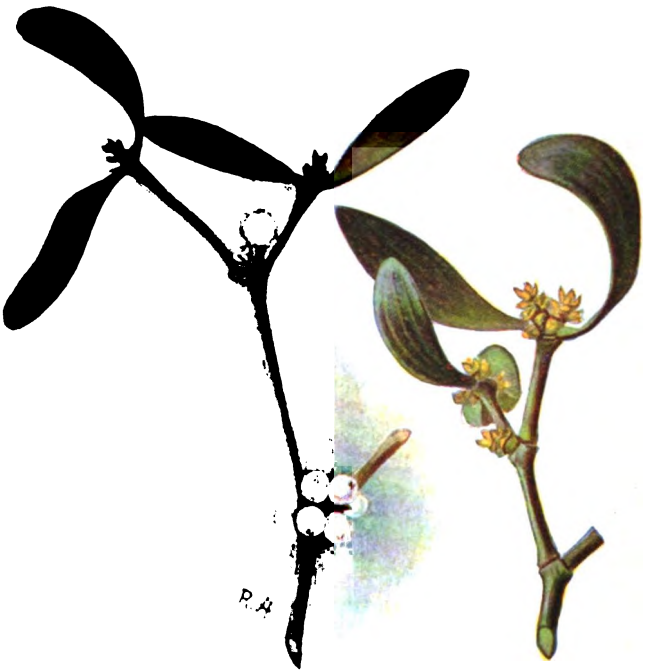


Fig. 616.—*Viscum album.* With flowers and fruits. (½ nat. size.)

Officjal.—*Santalum album*, the wood of which when distilled yields oleum santali. The wood is also of economic value.

Family 2. **Loranthaceae.**—Leafy semi-parasitic shrubs, living on the branches of trees. They are most abundant in the tropics, and, for instance in South America, add to the beauty of the forest by their brightly coloured flowers.

Loranthus europaeus, on Oaks in Europe. In Britain *Viscum album* (Fig. 616), the Mistletoe, occurs as an evergreen parasite on a number of trees. It has opposite, obovate leaves. Stem swollen at the nodes. The white berries are distributed by birds. The sucker, without a root-cap, emerging from the seed penetrates the cortex of the host to the wood, into which it cannot grow. Its tip is embedded in the new wood formed by the cambium of the host. Further growth in length of the sucker is effected by a zone corresponding in position to the cambium of the host.

Order 6. Polygoninae

Family 1. **Polygonaceae.**—For the most part perennial herbs, with hollow stems swollen at the nodes, and alternate, simple leaves. The membranous stipules of the latter are coherent to form a sheath or OCHREA protecting the terminal bud; when broken through by the growth of the stem, this remains as a tubular sheath around the lower part of the internode (Fig. 617).

Mainly natives of the N. Temperate zone.

GENERA.—*Rheum*, Rhubarb. This is an East Asiatic genus, with large, radical leaves and a large, spreading, paniculate inflorescence. Leaves simple, cordate-reniform, with palmate venation, sometimes more or less lobed. The flower has a perigone of two similar whorls, and two whorls of stamens, the outer whorl being double by chorisis; P 3+3, A 6+3, G (3). Nectar for visiting insects is secreted by the large scales of the disc. The triangular ovary becomes winged as it develops into the fruit (Fig. 618). Species of *Rheum* are cultivated as ornamental plants and as vegetables. *Rumex acetosa*, Sorrel, with sagittate leaves. The structure of the flowers of the hermaphrodite species of *Rumex* is similar to that of *Rheum*, but the inner whorl of stamens is wanting. The species of *Polygonum* have a perigone consisting of five coloured leaves and a varying number of stamens. The triangular fruits of *Fagopyrum esculentum* form Buckwheat (Fig. 571 *B*).

FIG. 617.—Leaf of *Polygonum amplexicaule* showing the ochrea, *st*. (½ nat. size.)

OFFICIAL.—The Rhizome of *Rheum officinale*, *Rh. palmatum*, and probably other species yields RADIX RHEI.

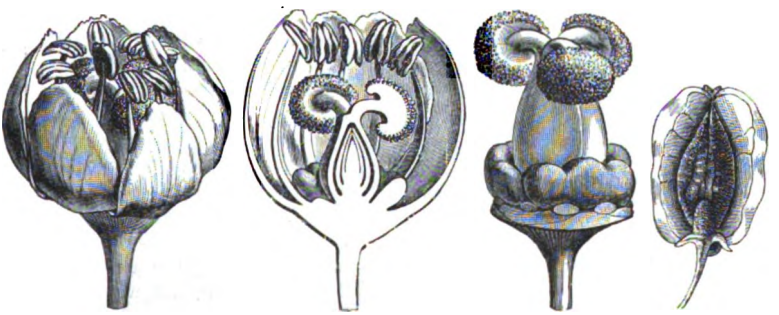


FIG. 618.—*Rheum officinale*. *A*, Flower; *B*, the same cut through longitudinally; *C*, gynaeceum with disc. *Rheum compactum*: *D*, fruit. (After LÜRSSEN, magnified.)

Order 7. Piperinae

Single family. **Piperaceae.**—The genus *Piper* is important. Flowers as a rule

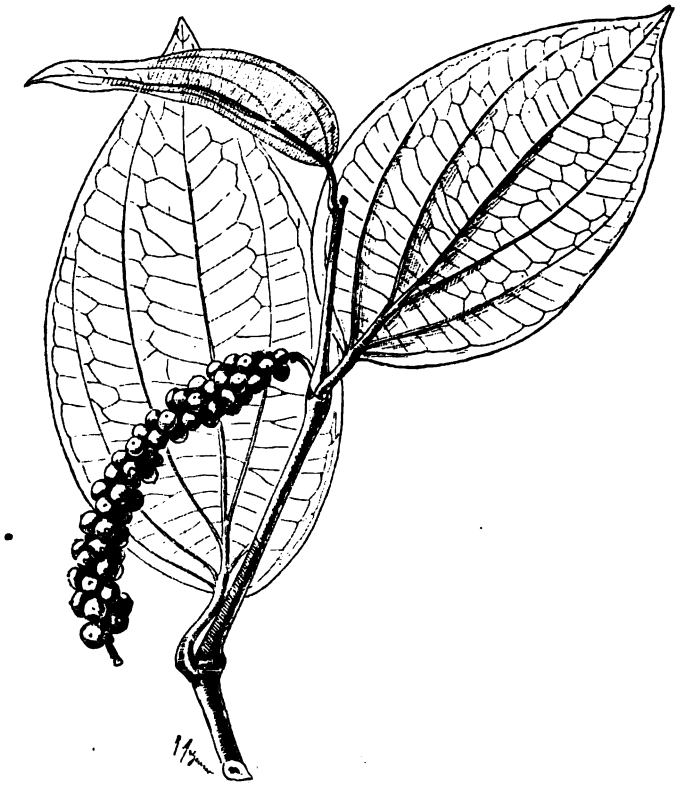


FIG. 619.—*Piper nigrum.* (½ nat. size.) *OFFICIAL.*

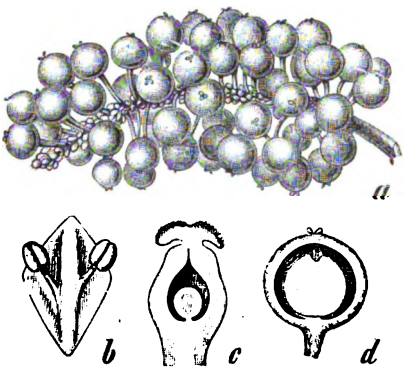


FIG. 620.—*Piper cubeba.* *a*, Infructescence; *b*, a male flower; *c*, a female flower in longitudinal section; *d*, fruit in longitudinal section. *OFFICIAL.* (After BERG and SCHMIDT.)

unisexual and without perianth, associated in spikes; typically trimerous but usually reduced. Ovary unilocular, ovule solitary, basal and atropous. Fruit drupe-like. The embryo is embedded in a small endosperm surrounded by a well-developed perisperm. The vascular bundles are scattered in the cross-section of the stem resembling the arrangement in Monocotyledons, but with secondary thickening.

Piper nigrum, from which the Peppers are derived, is the most important representative. This is a root-climber, native to the Malayan region, but now cultivated throughout the tropics (Fig. 619). The unripe

fruits provide black pepper, while white pepper is obtained from the ripe fruits after removal of the outer layers of the pericarp.

OFFICIAL.—*Piper Betle*, *Piper nigrum* and *Piper cubeba* (Fig. 620). The latter is a native of Java and is distinguished by the stalk-like base of the fruit from that of the Black Pepper. It provides CUBEBAE FRUCTUS.

The orders 8-10 constitute parallel series leading from the simplest flowers to the Dialypetalae, but are not directly connected with one another.

Order 8. Hamamelidinae

This includes the two Families **Hamamelidaceae** and **Platanaceae**.—Woody plants, with stipulate leaves. Flowers as a rule inconspicuous, without perianth and anemophilous. Conspicuous, entomophilous, flowers with a simple, or more rarely double, perianth also occur. Two carpels.

OFFICIAL.—STYRAX PRAEPARATUS from *Liquidambar orientalis*. HAMAMELIDIS CORTEX and FOLIA from *Hamamelis virginiana*.

Platanus orientalis and *P. occidentalis* are commonly planted as shade trees by the sides of streets.

Order 9. Tricoccae (20)

Family **Euphorbiaceae**.—The plants belonging to the Euphorbiaceae are of very diverse habit. The order includes herbs, shrubs, leafless succulent plants, trees with normal foliage, and others with scale leaves and assimilating phylloclades. The plants agree, however, in possessing unisexual, actinomorphic flowers, with a simple perianth or with no trace of the latter. Androecium diplostemonous or stamens numerous. The female flowers are especially characterised by the superior, trilocular

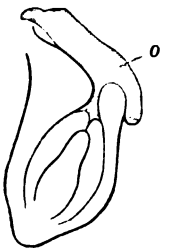


FIG. 621.—Ovule of *Euphorbia dioica* showing the obturator *o*. (After PAX in ENGLER-PRANTL.)

FIG. 622.—*Mercurialis annua* (½ nat. size). Male plant in flower and single male flower. Portion of a female plant, single female flower and fruit. *POISONOUS.*

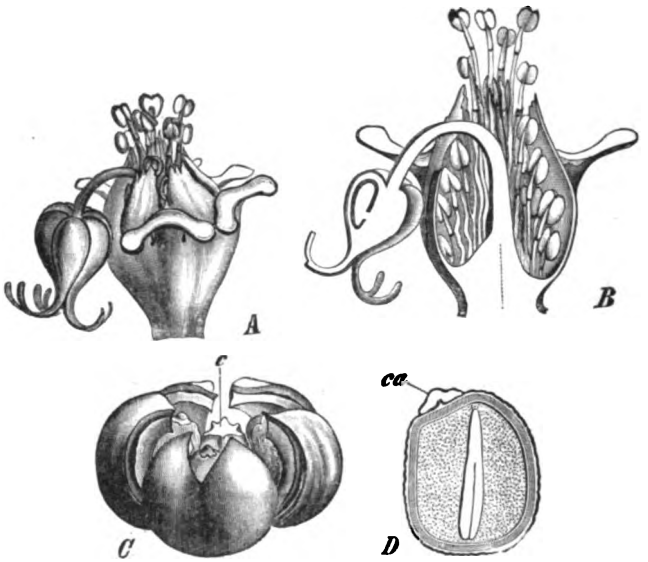


FIG. 623.—*Euphorbia Lathyris*. *A*, Cyathium (× 5). *B*, Cyathium cut through longitudinally (× 7). *C*, Fruit after dehiscence showing the central column (*c*). *D*, Seed in longitudinal section showing the embryo embedded in the endosperm; *ca*, caruncula (× 4). (*A-D* after BAILLON.)

ovary formed of three carpels; in each loculus are one or two pendulous ovules with a ventral raphe, and the micropyle directed upwards and outwards.

The micropyle is covered by a placental outgrowth called the obturator (Fig. 621); this assists in conducting and nourishing the pollen-tube, and disappears after fertilisation (cf. p. 573). The CARUNCULA, which is formed from the outer integument (Fig. 567 *B*),

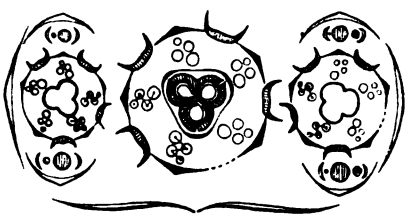


FIG. 624.—Diagram of a dichasial branch of *Euphorbia*, with three cyathia, only the middle one of which has a fertile female flower. (After EICHLER.)

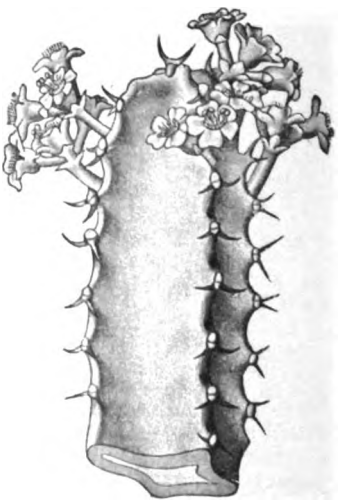


FIG. 625.—*Euphorbia resinifera*. (Nat. size. After BERG and SCHMIDT.)

persists on the other hand in the seed; the separation of the latter from the placenta is assisted by it. The fruit is a capsule, the outer walls of which contract elastically away from a central column, and thus open the loculi.

The plants of this family are distributed over the whole earth. IMPORTANT GENERA.—Many Euphorbiaceae are dioecious or monoecious, and have flowers of relatively simple construction. Thus *Mecurialis* (Fig. 622), two species of which

FIG. 626.—*Ricinus communis*, greatly reduced. (After BAILLON.) *POISONOUS* and *OFFICIAL*.

occur in Britain, is characterised by its bicarpellary ovary. *Croton* is a tropical genus including valuable official plants, *C. Eleuteria* and *C. Tiglium*; the male flowers have a double, the female flowers a single perianth. In the Spurges (*Euphorbia*), of which there are several British species, a number of the extremely simply constructed flowers are grouped in a complicated inflorescence termed a CYATHIUM (Figs. 623-625). This consists of a naked, terminal, female flower, borne on a long bent stalk surrounded by a number of groups of male flowers. Each of the latter is stalked and consists of a single stamen, the limit between which and the flower-stalk is distinguishable. In some cases the female flower

and each male flower are provided with a small perianth. The whole cyathium, which is an inflorescence, is always enclosed by five involucral bracts; alternating with these are four nectar-secreting glands, the presence of which increases the likeness between the cyathium and a flower. The fifth gland is wanting, and the inverted female flower hangs down in the gap thus left. Between the groups of male flowers which stand opposite to the bracts (Fig. 624) are branched hairs which are visible when the cyathium is cut through longitudinally (Fig. 623 *B*). The cyathia are usually grouped in dichasia, and these in turn form an umbellate inflorescence, with three to many branches. It often happens that the female flower is only developed in some of the cyathia, remaining rudimentary in the others. Many species of *Euphorbia*, especially the African species, are succulent-stemmed plants resembling *Cacti* in general appearance (Fig. 625).

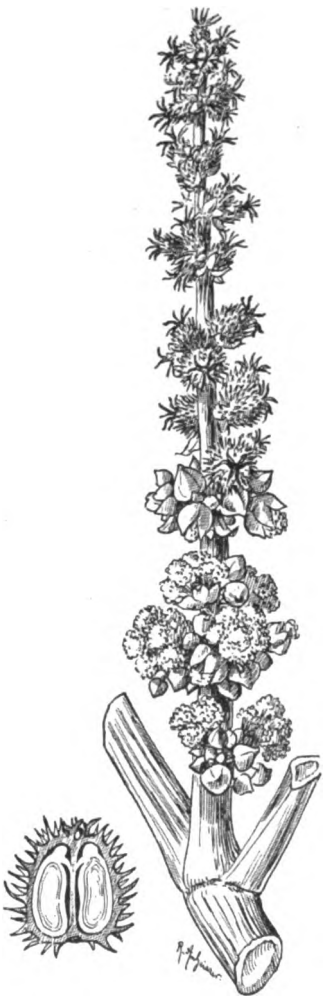


Fig. 627.—*Ricinus communis*. Inflorescence (½ nat. size); young fruit cut through longitudinally. *Official.*

Euphorbia, like many but not all the other plants of the family, contains a milky juice, which is secreted in non-septate latex-tubes. This juice, which in many cases is poisonous, exudes wherever the plant is wounded.

An important constituent of the latex of species of *Hevea* (*H. Sieberi*, *discolor*, *rigidifolia*, *paucifolia*, *lutea*, *guyanensis*, *Spruceana*) is CAOUTCHOUC (cf. [19]). As Para Rubber obtained in the tropics of South America, especially in the Amazon Region, this affords about one-half of the total rubber supply. In addition *Manihot Glaziovii*, another South American plant of this order, which yields Ceara Rubber, must be mentioned. A nearly related plant, *Manihot utilissima*, provides in its tuberous roots a very important food in the tropics. The starch obtained from these roots forms mandioc or cassava meal, the finest varieties of which, as tapioca or Brazilian arrowroot, are of commercial importance. The shrub, which is a native of Brazil, is now cultivated throughout the tropics.

Ricinus communis (Fig. 626) is a tall shrub of tropical Africa. In our climate it is annually killed by the frost. The hollow stem bears large palmately-divided leaves. The terminal inflorescences (Fig. 627) are overtopped by vegetative lateral branches. The male flowers, situated towards the base, have a membranous calyx of 4-5 sepals, enclosing the branched stamens; the end of each branch bears a theca. The female flowers, nearer the summit of the inflorescence, have 3-5 sepals and a large tripartite ovary. The latter is

covered with warty prickles, and bears three large, bifid, red stigmas. In each loculus of the fruit is a mottled seed with a whitish caruncula.

OFFICIAL.—*Croton Eleuteria* (Bahamas) yields CASCARILLA. *C. tiglium* (East Indies), OLEUM CROTONIS. OLEUM RICINI, Castor Oil, is obtained from *Ricinus communis*.

Order 10. Centrospermae

Plants with as a rule hermaphrodite flowers which approximate to the typical dicotyledonous flower.

Family 1. **Chenopodiaceae.**—Perennial or annual herbs, rarely small woody plants, with alternate leaves. Flowers typically pentamerous, with a single whorl in both perigone and androecium; P 5, A 5, G (2-5). Stamens opposite the perianth leaves. Reduced, unisexual flowers are not infrequent. The unilocular ovary contains a basal, campylotropous ovule. Fruit, a nut. Seed with a curved embryo bent around the floury perisperm.

Many of the Chenopodiaceae are strand plants or occur on soils containing a large amount of salt, such as the great Asiatic salt steppes and deserts. The Spinach (*Spinacia oleracea*) and the Summer Spinach (*S. glabra*) are used as vegetables. The Sugar Beet (*Beta vulgaris*, var. *rapa*) is a plant of great economic importance. It is a biennial plant, and in the first season forms a thick, swollen root bearing a bud consisting of a number of thick-stalked, entire, succulent, and often crisped leaves. From this rosette of leaves there springs in the second season a highly branched panicle, bearing the inconspicuous greenish flowers. Ovary formed of three carpels. At the end of the first season the root contains cane-sugar as a reserve material, which at this stage is extracted from the plant. By constant selection the percentage of sugar is raised from 7-8 % to an average of 14 %; it may, however, reach 21-26 %. The original form of the Sugar Beet is *Beta patula*. *Chenopodium* and *Atriplex* are common weeds near human dwellings.

Family 2. **Caryophyllaceae.**—Annual or perennial herbs, with simple, linear, usually opposite leaves; flowers typically pentamerous, with calyx and corolla. Two whorls of stamens, obdiplostemonous. Unilocular or incompletely septate ovary. K 5, C 5, A 5 + 5, G (5) (Fig. 630). Fruit, a capsule. Seeds numerous, embryo curved around the floury perisperm.

Cerastium and *Stellaria* have white flowers and bifid petals, and are conspicuous, early-flowering forms. Species of *Dianthus*, Pinks, have frequently attractive colours and scent, and occur in dry sunny situations. *Agrostemma Githago* (Fig. 628), Corn-cockle, is a hairy plant with pink flowers; it is a common weed in corn-fields. Since its seeds are poisonous, their mixture with the grain may have serious results. *Saponaria officinalis* is a herb attaining the height of a metre, with opposite, broad leaves and rose-coloured flowers. The saponin contained in all parts of the plant renders it poisonous (Fig. 629).

Family 3. **Aizoaceae.** Perennial herbs or small shrubs, usually with succulent leaves. Flowers hermaphrodite; with simple perianth or with a calyx and a polypetalous corolla derived from modified stamens. Stamens numerous. Carpels 2-∞; united to form the hygroscopic capsule.

Xerophytic plants of hot countries. *Mesembryanthemum*; a large genus, especially in Africa.

Family 4. **Cactaceae.**—For the most part leafless plants with succulent stems, natives of America. In size they range from very small to gigantic forms. Flowers

Fig. 628.—*Agrostemma Githago.* Flowering shoot and fruit (½ nat. size). *Poisonous.*

hermaphrodite, actinomorphic, less commonly dorsiventral. Perianth of many members, spirally arranged and showing a gradual transition from the calyx to the corolla. Stamens and carpels numerous. Ovary inferior, unilocular, with numerous parietal placentas. Ovules with long stalks. Fruit, a berry, the succulent tissue being largely derived from the stalks of the seeds.

Peireskia and some species of *Opuntia* possess leaves. Other species of *Opuntia*

have flattened branches (Fig. 197). *Cereus* (Fig. 631), *Echinocactus*, with longitudinal ridges on the stem; *Mammillaria* has free projections (mamillae). The numerous groups of spines on the shoots, ribs, or separate mamillae correspond to axillary shoots, the subtending leaves of which are reduced, while the leaves of the expanded axis of the axillary shoot are metamorphosed into spines (Fig. 631).

Cactaceae form a dominant constituent of the vegetation in the dry south-western regions of the United States and in Mexico. They are also widely distributed in the West Indies and South America. A similar habit is found in some Euphorbiaceae and Asclepiadaceae living under corresponding climatic conditions (cf. p. 174). There are numerous epiphytic Cactaceae, especially species of *Rhipsalis*, *Epiphyllum*, and *Phyllocactus*, which clothe the branches of trees and affect the general aspect of the vegetation. *Opuntia ficus indica* has become naturalised in the Mediterranean region. The fruits of this species and of others of the genus are edible, and the plants are cultivated as fruit-trees. Some Cactaceae, such as *Anhalonium*, contain highly poisonous alkaloids and saponin. The Cochineal insect is grown upon species of *Opuntia* and *Nopalea* (*N. coccinellifera*).

FIG. 629.—*Saponaria officinalis* (½ nat. size). *POISONOUS.*

B. DIALYPETALAE

Flowers with calyx and corolla.

Order 11. Polycarpicae

Hermaphrodite, usually brightly coloured flowers, with an elongated receptacle on which the free perianth segments, the stamens and the apocarpous carpels are spirally arranged; the carpels are indefinite in

number and may be very numerous. The separation of calyx and corolla is frequently indistinct, and in some cases (*e.g. Calycanthus*) even the foliage leaves pass with their spiral arrangement into the bracts of the flower. The stamens have frequently a leaf-like form with the connective continued beyond the anthers, or forming a leafy expansion. The stigma terminates the carpel without a definite style. The pollination is by means of insects; in some primitive forms by

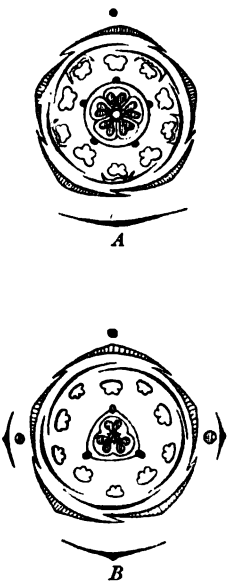


FIG. 630.—Diagrams of the Caryophyllaceae. *A*, *Viscaria*, septa present in the lower part of the ovary. *B*, *Silene*, septa absent. (After EICHLER.)

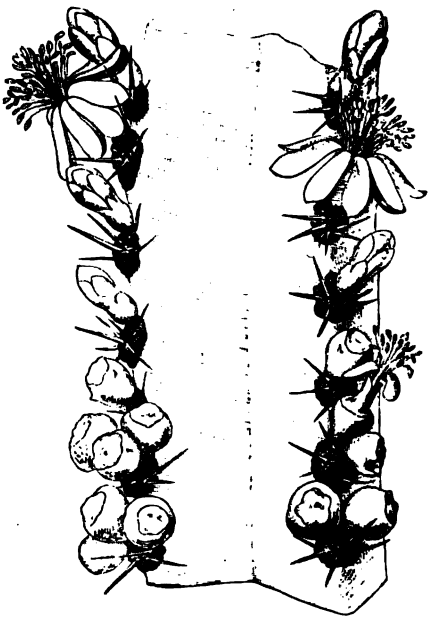


FIG. 631.—*Cereus geometrizans*. Two of the ribs or ridges of a five-ribbed stem bearing flowers and fruits (⅓ nat. size).

beetles. The structure of the wood in some cases approaches that of the Coniferae.

The simplest Monocotyledons (*Helobiae*) exhibit an unmistakable relationship to this order; they agree in the numerous stamens and the apocarpous pistil. It is, however, to be noted that by no means all the plants of the families united in this order exhibit the above characters in the same degree. The characteristic features may indeed be completely wanting, though the existence of intermediate forms leaves no doubt that the genera in question must be classed here.

Family 1. **Nymphaeaceae.**—Aquatic plants with submerged or floating leaves, the latter often of very large size; the vegetative organs contain latex and thus indicate a relationship with the Papaveraceae (Figs. 632-634).

Nymphaea alba, the White Water Lily (Figs. 632, 633), has large floating leaves and white flowers, protected by firm green sepals. Within the corolla comes the

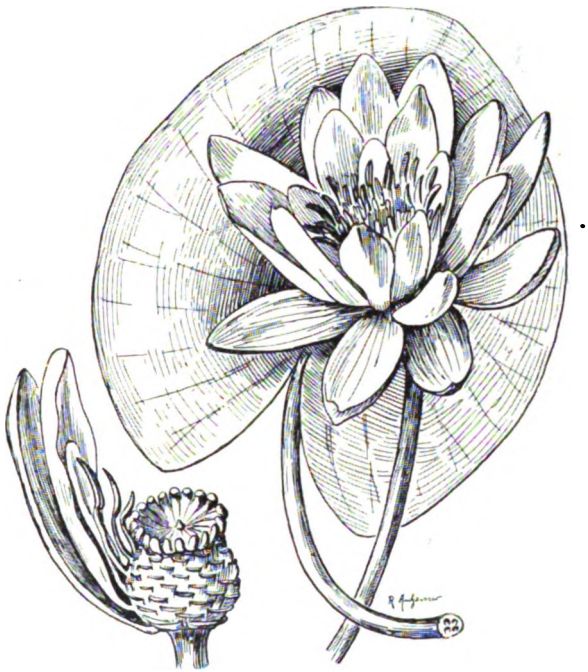


FIG. 632.—*Nymphaea alba* (⅛ nat. size.) The spiral arrangement of the stamens and petals is shown by their insertions on the ovary to the left.

zone of numerous stamens and the inferior ovary composed of numerous, coherent carpels. The spiral arrangement of the members of the perianth and androecium

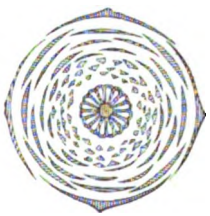
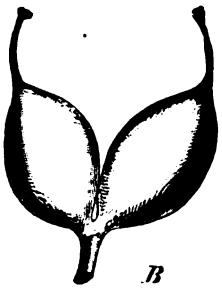


FIG. 633. — *Nymphaea*. Floral diagram. (After NOLL.)



A B

FIG. 634.—*A*, Floral diagram. *B*, Fruit of *Cabomba aquatic* showing two carpels developed as partial fruits. (× 4 After BAILLON.)

is seen by the scars of their insertion when they are removed from the inferior ovary (Fig. 632), and in the floral diagram (Fig. 633). In *Nuphar* the ovary is

superior and the small petals bear nectaries ; the conspicuous calyx renders the flower attractive. In the American genus *Cabomba* (Fig. 634) the flowers are trimerous and the pistil is apocarpous. The finely divided, submerged leaves differ in appearance from the entire, floating leaves. The carpels are also free in *Nelumbium*, both the leaves and flowers of which are raised above the surface of the water. *Victoria regia* from the Amazon, and *Euryale ferox* from tropical Asia, have gigantic floating leaves ; they are often cultivated in Botanic Gardens. The flowers of the former are beetle-pollinated, while the latter is autogamous.

FIG. 635. — *Myristica*. Transverse section of seed. *sa*, *sch*., Seed-coat ; *end*, endosperm ; *pe*, perisperm. OFFICIAL.

Family 2. **Magnoliaceae.**—The plants of this family are all woody with large terminal flowers. The perianth leaves without distinction into sepals and petals, the numerous stamens and the apocarpous carpels are all spirally arranged in ascending order on the elongated floral axis. The stigma terminates the carpel without intervening style. Oil-cells in the stem and leaves. Pollen-grains with one germ-pore are characteristic of the family. *Drimys* and *Zygogynum* have wood without vessels, like the Coniferae. *Magnolia* and *Liriodendron* (Tulip tree) are frequently cultivated.

OFFICIAL. — ANISI STELLATI FRUCTUS, Star-anise, is obtained from *Illicium verum* (China). The fruits of *Illicium religiosum* (Japan) are poisonous.

Family 3. **Anonaceae.** —Woody plants of the tropics, with spirally arranged stamens and apocarpous gynaeceum ; seeds with ruminated endosperm.

Family 4. **Myristicaceae.**—Resembles the preceding family, but the dioecious flowers are more simply constructed (Figs. 635, 636).

FIG. 636.—*Myristica fragrans*. *1*, Twig with male flowers (½ nat. size). *2*, Ripe pendulous fruit opening. *3*, Fruit after removal of one-half of the pericarp, showing the dark brown seed surrounded by the ruptured arillus. *4*, Kernel freed from the seed-coat. OFFICIAL.

OFFICIAL.—MYRISTICA, Nutmeg. The seed of *Myristica fragrans* divested of its testa.

Family 5. **Calycanthaceae.** —These plants show a continuous sequence from

the foliage leaves to the numerous free perianth leaves, stamens, and carpels borne on the depressed floral axis. The connection of the Rosaceae may perhaps be here.

Family 6. **Ranunculaceae.**—The plants belonging to this family are annual herbs (*Myosurus*), more commonly perennial herbs (*Caltha*) or rarely woody plants (species of *Paeonia*) with alternate, exstipulate leaves. Flowers hermaphrodite, the members in many cases arranged

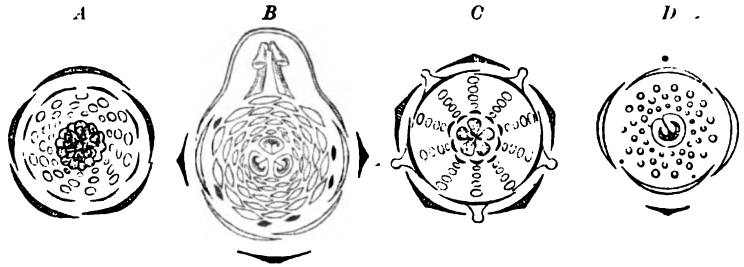


FIG. 637.—Floral diagrams of Ranunculaceae. *A*, *Adonis autumnalis*. *B*, *Aconitum napellus*. *C*, *Aquilegia vulgaris*. *D*, *Cimicifuga racemosa*. (After EICHLER.)

spirally; this is very evident in *Myosurus*. Perianth either forming a simple or double perigone (*Aconitum*) or differentiated into calyx and corolla (*Ranunculus*). Stamens indefinite. Pollen-grains with at least three places of exit for the pollen-tubes. Carpels three to indefinite, borne on the convex receptacle (Fig. 638), and forming an apocarpous, superior ovary. Ovules, borne on the ventral suture,

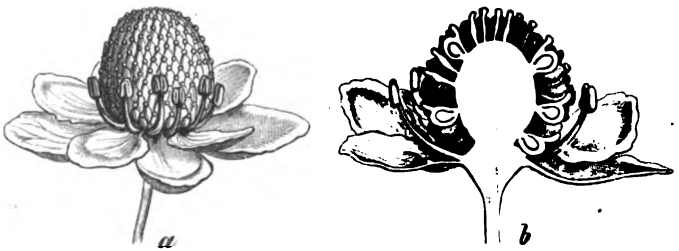


FIG. 638.—*a*, Flower of *Ranunculus sceleratus*; *b*, the same, cut through longitudinally; magnified. (After BAILLON.)

singly or in numbers. The partial fruits are follicles (*Paeonia*), achenes (*Anemone*), or berries (*Hydrastis*). Seed with a small embryo enclosed within the large, oily endosperm.

IMPORTANT GENERA.—Many of our commonest meadow and woodland plants belong to this order. They are all in greater or less degree poisonous. A number of species of *Ranunculus*, characterised by the usually yellow flowers, convex receptacle, and fruit composed of numerous free achenes, occur in Britain. The petals have a nectary at the base. Leaves palmately divided more or less deeply. *R. sceleratus* is very poisonous (Figs. 638, 639). *R. arvensis* with large, spiny

FIG. 639.—*Ranunculus sceleratus* (½ nat. size). *POISONOUS.*

FIG. 640. — *Ranunculus arvensis*. Carpel in longitudinal section. (Enlarged. After BAILLON.)

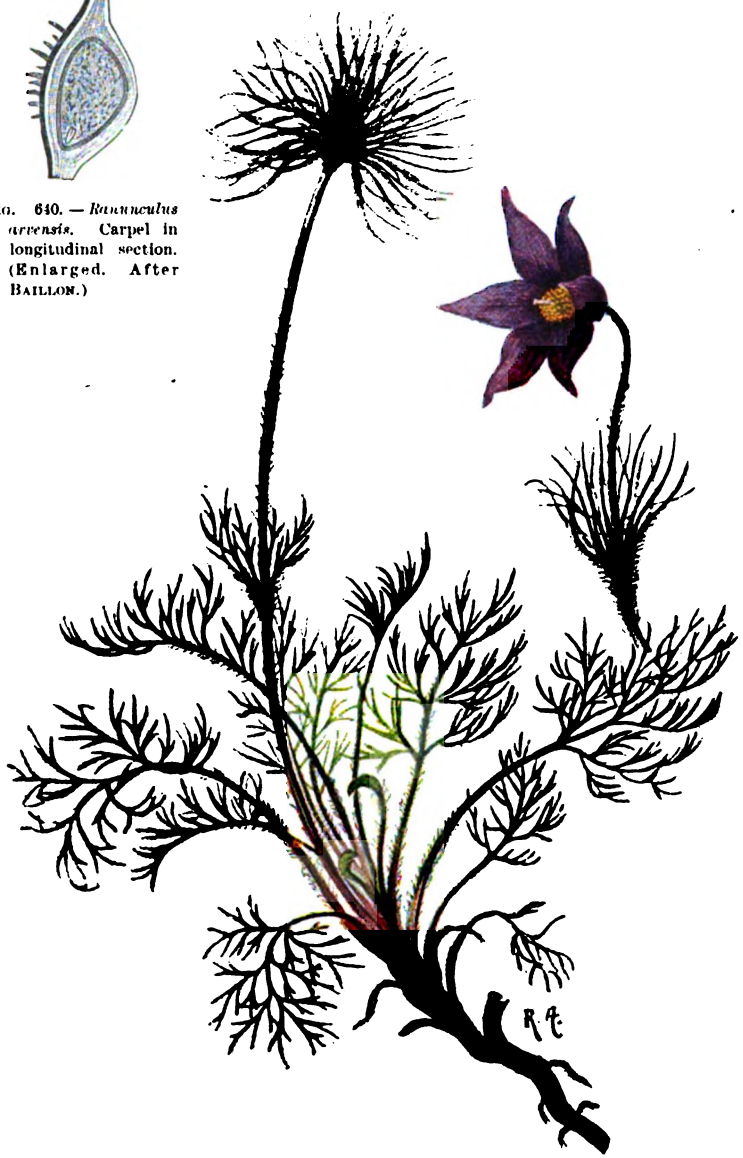


FIG. 641.—*Anemone Pulsatilla* (½ nat. size). *POISONOUS.*

achenes or nutlets (Fig. 640). The aquatic species of *Ranunculus*, belonging to the section *Batrachium*, are often heterophyllous (Fig. 35), the floating leaves serving to support the flowers above the surface of the water.

Species of *Anemone* are also widely distributed in Europe. *A. nemorosa* occurs commonly in woods and is one of our early spring flowers. It has a horizontal, subterranean rhizome, which terminates in a flower, the further growth of the plant being carried on by a lateral shoot. Perianth simple, petaloid. All species of *Anemone* have, at a greater or less distance from the perianth, a whorl of, usually, three leaves forming an involucre (Fig. 641). In *A. hepatica* this stands just below the perianth and thus resembles a calyx. All the species are to some extent poisonous, especially *A. Pulsatilla* (Fig. 641). The plants of the genus *Clematis* are mostly woody and differ from other Ranunculaceae in having opposite leaves. Many species are cultivated. *C. vitalba* is one of our few native lianes. The achenes of the species of *Clematis* and of many kinds of *Anemone* are provided with hairy or feathery appendages, which facilitate their distribution by the wind. *Caltha palustris*, the Marsh Marigold (Fig. 642), is one of the most conspicuous spring flowers in damp meadows. Perianth simple, bright yellow. Leaves cordate or reniform, short-stalked, with erect sheathing base. Fruit, as in the species of *Helleborus* that flower in the winter, composed of follicles. The Monkshood (*Aconitum napellus*) (Figs. 643, 644) is a stately perennial herb with underground tubers and occurs most commonly in alpine meadows. The leaves are palmately divided, the segments being in turn pinnately lobed. Inflorescence a dense raceme, reinforced by lateral inflorescences standing in the axils of the upper leaves. Flowers zygomorphic. One of the five dark-blue sepals is helmet-shaped, and protects two long-stalked, tubular, two-lipped nectaries, which correspond to petals. The remaining petals are wanting or are

FIG. 642.—*Caltha palustris* (⅓ nat. size). *Poisonous.*

reduced to inconspicuous, narrow structures. *Aconitum Lycoctonum* has smaller

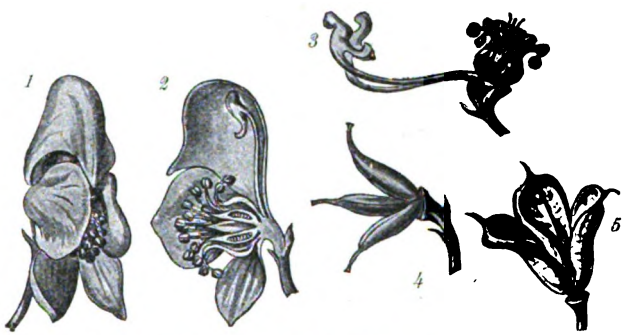


FIG. 644.—*Aconitum napellus* (nat. size). *1*, Flower seen obliquely from in front. *2*, Flower in longitudinal section. *3*, The nectaries, formed from petals, and the androecium after the perigone has been removed. *4*, Fruit composed of three apocarpous carpels. *5*, Follicles opened.

FIG. 643.—*Aconitum napellus* (¼ nat. size). *OFFICIAL* and *POISONOUS*.

yellow flowers of similar construction. All the species are poisonous. *Aquilegia*,

Delphinium, and *Paeonia* are favourite ornamental plants with showy flowers. In *Actaea* and *Hydrastis* the fruit is a berry.

OFFICIAL.—ACONITI RADIX is obtained from *Aconitum napellus*. STAPHISAGRIAE SEMINA from *Delphinium staphisagria*. HYDRASTIS RHIZOMA from the North American *Hydrastis Canadensis* (Fig. 645), a perennial herb which sends its subaerial shoots up from the subterranean rhizome; the base of the shoot has keeled scale-leaves in two ranks. The flowers are solitary and terminate the shoots, each of which bears two foliage leaves. The simple white perianth falls when the flower opens. The androecium and the apocarpous gynaeceum consist of numerous members. The fruit consists of numerous, small berries, each of which includes 1-2 seeds. The alkaloid HYDRASTINE is obtained from the rhizome.

FIG. 645.—*Hydrastis canadensis* (½ nat. size). The apocarpous fruit to the left. OFFICIAL.

The further families of the Polycarpicae show a limitation to three in the whorls of the simple, or more usually double, perianth and of the stamens.

Family 7. **Berberidaceae** has only one carpel, while there are three carpels in Family 8, **Menispermaceae**. In *Berberis vulgaris* the leaves on the shoots of unlimited growth are transformed into spines.

OFFICIAL.—PODOPHYLLI RHIZOMA obtained from the N. American Berberidaceous plant, *Podophyllum peltatum* (Fig. 646), *P. emodi*, *Berberis Aristata*, CALUMBAE RADIX from the twining Menispermaceous plant *Jateorhiza columba*.

Family 9. **Lauraceae.**—Flower also composed of trimerous whorls; perianth 3+3; stamens 3+3. The three stigmas of the single, one-seeded pistil indicate its origin from three coherent carpels. Fruit, a berry or drupe. Anthers valvate. Aromatic trees or shrubs with entire leathery leaves, which usually persist for several seasons. Only *Sassafras* (Fig. 647), which has three-lobed leaves as well as simple ones, sheds its foliage annually. *Laurus nobilis*, the Laurel, is a

dioecious, evergreen tree of the Mediterranean region, which was well known in the early period of the Grecian civilisation; it is frequently grown in cool greenhouses (Figs. 649, 650). Large plantations are grown at the Lake of Garda, where the oil is extracted, and here the trees ripen their oval, blackish-blue drupes in October. The genus *Cinnamomum* includes a number of economically important trees such as the Camphor tree from Japan and China and the Cinnamon tree from China and Ceylon. The latter is a stately evergreen with smooth, leathery leaves and inconspicuous, greenish flowers in axillary inflorescences. *Persea gratissima* (Fig. 648) is a native of tropical Mexico, and is frequently cultivated as a fruit tree in the tropics. Its fruit is known as the Avocado Pear. Species of *Cassytha*,

FIG. 646.—*Podophyllum peltatum* (½ nat. size). OFFICIAL. (From *Nat. Pflanzenfamilien.*)

the only genus of the family including herbaceous species, occur throughout the tropics as parasites resembling *Cuscuta*.

OFFICIAL.—CAMPHORA, Camphor, is obtained from *Cinnamomum Camphora*. CINNAMOMI CORTEX and OLEUM CINNAMOMI from *Cinnamomum zeylanicum*. *Cinnamomum Oliveri*.

Family 10. **Aristolochiaceae**.—The zygomorphic flowers (Fig. 534) have a simple coherent perianth and the androecium and gynaeceum united to form a gynostemium. OFFICIAL.—*Aristolochia serpentaria*, *A. reticulata*.

The parasitic **Rafflesiaceae** and the insectivorous families of the **Cephalotaceae**, **Sarraceniaceae**, **Nepenthaceae** and **Droseraceae** may best be placed with the Polycarpicae.

Order 12. Rhoeadinae

Herbs, or more rarely shrubs, with alternate, exstipulate leaves. Flowers hermaphrodite, cyclic; whorls usually bimerous. Ovary

FIG. 647.—*Sassafras officinale.* (¼ nat. size. After BERG and SCHMIDT.) *1*, Male inflorescences on a still leafless branch. *2*, Fruits on a leafy shoot. *3*, Male flower. *4*, Female flower. *5*, *6*, Closed stamens of the two outer whorls. *7*, Opened stamen of the innermost whorl. *8*, Ovary showing the style and the ovule.

FIG. 648.—Floral diagram of *Persea*. (After EICHLER.)

superior, unilocular. Placentas on the united margins of the carpels, projecting more or less into the cavity (Fig. 651). Stigmas commisural, *i.e.* situated immediately over the sutures. Dehiscence of the fruit by separation of the middle portions of the carpels from the persistent placentas.

Family 1. **Papaveraceae.**—This family connects the order to the Polycarpicae by such characters as the presence of laticiferous tubes

FIG. 649.—*Laurus nobilis* with male flowers. (½ nat. size.)

FIG. 650.—*Laurus nobilis* with fruits. (½ nat. size.)

(Nymphaeaceae), occurrence of trimerous flowers in *Bocconea* (Berberidaceae), the stigmas situated directly above the carpels and the occasional occurrence of an apocarpous gynaeceum (*e.g. Platystemon*). The increase in number of stamens is brought about by chorisis; they are cyclic. The seeds have abundant endosperm. *Chelidonium majus*, Celandine, has yellow latex and a bicarpellary ovary. A number of species of *Escholtzia*, *Argemone*, and *Papaver* are cultivated as ornamental plants. *Papaver Rhoeas*, the Poppy (Fig. 652), is a common weed in corn-fields or dry meadows. The bent position of the flower-bud is characteristic of many Papaveraceae. *Papaver somniferum*, which is of oriental origin, has abundant white latex. The plant has a glaucous bloom and, except on the flower-stalks, which bear a few bristly hairs, is glabrous. Leaves sessile, margin irregularly serrate or lobed. Petals violet or white with a dark patch at the base. Ovary unilocular, incompletely septate by the projection inwards of the numerous placentas. Fruit ripens erect on the

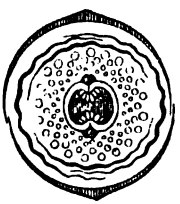


FIG. 651.—Floral diagram of *Glaucium* (Papaveraceae). (After EICHLER.)

FIG. 653.—Floral diagram of *Corydalis cava*. (After EICHLER.) At the base of the stamen standing above the spur is a nectary.

FIG. 652.—*Papaver Rhoeas*. (½ nat. size.) *OFFICIAL.*

peduncle. In *Papaver* the separation of the central portion of each carpel from the placentas at dehiscence is limited to the tips of the carpels. These portions bend outwards just below the flat stigmatic expansion, and the kidney-shaped seeds are

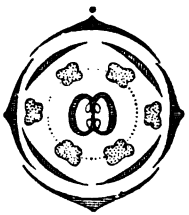


FIG. 654.—Cruciferae. Floral diagram (*Brassica*).

FIG. 655.—*Cardamine pratensis*. Flower with perianth removed. (× 4. After BAILLON.)

thrown out of the small openings when the capsule, borne on its long stalk, is moved by the wind.

OFFICIAL.—*Papaver somniferum*, the Opium Poppy, yields PAPAVERIS CAPSULAE and OPIUM. *Papaver Rhoeas* yields RHOEADOS PETALA.

Family 2. **Fumariaceae.**—This small family is of interest on account of the

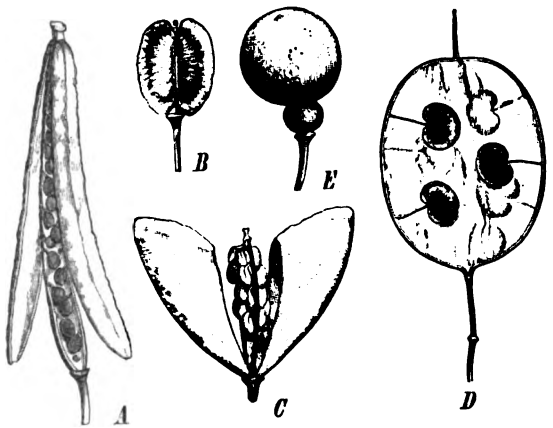


FIG. 656.—Cruciferous fruits. *A*, *Cheiranthus cheiri*; *B*, *Lepidium sativum*; *C*, *Capsella bursa pastoris*; *D*, *Lunaria biennis*, showing the septum after the carpels have fallen away. *E*, *Crambe maritima*. (After BAILLON.)

occurrence of transversely zygomorphic flowers in *Corydalis* (Fig. 653) and a bi-symmetrical corolla with two spurs in *Dicentra spectabilis*. The fruits are nutlets in *Fumaria* and capsules in *Corydalis* and *Dicentra*. Seeds with endosperm.

Family 3. **Cruciferae** (21).—This family is mainly distributed in

the northern hemisphere. Annual, biennial, or perennial herbs without milky juice. Inflorescence racemose, usually without bracts or bracteoles. Flowers actinomorphic, always lateral, composed of bimerous whorls. Floral formula, K 2 + 2, C 4, A 2 + 4, G (2) (Fig. 654). The outer whorl of sepals stands in the median plane; the four petals alternate with the sepals. The two outer stamens are shorter than the four inner ones which stand in the median plane. The latter correspond

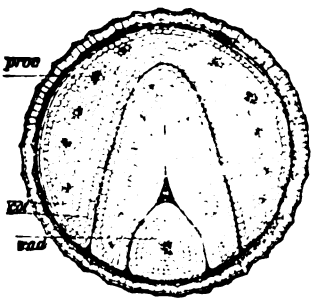


FIG. 657.—Transverse section of the seed of *Brassica nigra*. *rad*, radicle; *cot*, cotyledons; *vasc*, vascular bundles. (After MOLLER.)

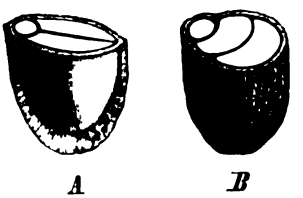


FIG. 658.—Seeds of Cruciferae cut across to show the radicle and cotyledons. *A*, *Cheiranthus cheiri* (× 8); *B*, *Sisymbrium alliaria* (× 7). (After BAILLON.)

FIG. 659.—*Brassica nigra*. (¼ nat. size.) OFFICIAL.

to two stamens branched to the base. The carpels form a superior, usually pod-like, ovary, which is divided into two chambers by a false septum stretching between the parietal placentas (Fig. 656 *D*). The fruit opens by the separation from below upwards of the main portion of each carpel, leaving the seeds attached by their stalks to the central portion formed by the placentas together with the false septum. Rarely the fruit is indehiscent (*e.g. Isatis*). Embryo

curved. Endosperm wanting or reduced to a single layer of cells coherent with the seed-coat (Figs. 657, 658).

The number of species and their abundance make the Cruciferae one of our most important native families of flowering plants. Their brightly coloured, mostly yellow flowers render them conspicuous in various situations and at all periods of the year. The nectaries, which are borne on the receptacle at the base of the stamens, also show that the flowers are entomophilous. The family includes a number of economic plants and others cultivated for their flowers.

FIG. 660.—*Capparis spinosa*. Flowering branch and a young fruit borne on the gynophore. (½ nat. size.)

Cheiranthus Cheiri, the Wallflower (Figs. 656 *A*, 658 *A*). *Matthiola*, the Stock. Numerous species of *Brassica* have been long in cultivation; *B. oleracea*, the Wild Cabbage, in its various forms—(*a*) *sylvestris*, which occurs on the coasts of Northern Europe and is to be regarded as the wild form; (*b*) *acephala*, Borecole or Kale; (*c*) *gonglyodes*, Turnip-rooted Cabbage; (*d*) *gemmifera*, Brussels Sprouts; (*e*) *sabauda*, Savoys; (*f*) *capitata*, the Cabbage; (*g*) *botrytis*, Cauliflower and Broccoli. *Brassica campestris*, with the cultivated forms—(*a*) *annua*, (*b*) *oleifera*, (*c*) *rapifera*. *Brassica napus*, the Turnip—(*a*) *annua*, (*b*) *oleifera*, (*c*) *napobrassica*. *Brassica nigra*, Black Mustard (Figs. 657, 659), an annual plant derived from the eastern Mediterranean region, was cultivated even in ancient times. The radical leaves are long-stalked and lyrate with rounded terminal lobes; on ascending the copiously-branched stem they become lanceolate and gradually smaller. The plant is glabrous except for some bristly hairs on the upper surface of the leaf. Inflorescence a raceme; the bright yellow flowers stand out from the main axis, while the developing fruits are erect and applied to the axis. *Sinapis alba*, White Mustard, is a hairy plant, distinguishable from the Black Mustard by the long broadly-beaked fruits, the valves of which bear coarse bristly hairs. The fruits project from the axis of the inflorescence. The seeds are yellowish-white and twice as large as those of *Brassica nigra*. *Anastatica hierochuntica*, Rose of Jericho, is an annual desert plant of N. Africa characterised

by the hygroscopic movements of its branches (cf. p. 333). *Crambe* (Fig. 656 *E*), with the lower portion of the siliqua sterile, and *Cakile* are thick-leaved, strand plants. *Raphanus sativus*, the Radish. *Vesicaria*, *Aubrietia*, *Draba*, *Lunaria* (Fig. 656 *D*). *Cochlearia officinalis*, Scurvy Grass. *Erophila*, *Iberis* with somewhat zygomorphic flowers. *Capsella bursa pastoris*, Shepherd's purse (Fig. 656 *C*). *Isatis tinctoria*, Woad.

OFFICIAL.—SINAPIS NIGRAE SEMINA, from *Brassica nigra*. ARMORACIAE RADIX, from *Cochlearia Armoracia*.

Family 4. **Capparidaceae.**—*Capparis spinosa* is a small shrub occurring on rocky ground in the Mediterranean region. The leaves are simple with short, recurved, spiny stipules. The actinomorphic flowers are axillary and solitary; the androecium by chorisis consists of numerous members. In this respect and in the presence of a gynophore which raises the pistil above the rest of the flower (Fig. 660), there are differences from the Cruciferae. The fruit is a berry which reaches the size of a plum and contains numerous seeds. Capers are prepared from the young flower buds.

Order 13. Cistiflorae

The plants belonging to this order are characterised by their usually regular, pentamerous flowers; the stamens are increased in number by chorisis, or when

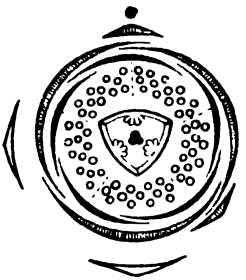


FIG. 661.—Floral diagram of *Helianthemum vulgare* (Cistaceae). (EICHLER.)

FIG. 662.—Floral diagram of *Viola*. (After NOLL.)

FIG. 663.—*Thea chinensis*. Flowering shoot (⅓ nat. size); fruit and seed.

the separation of the branches is incomplete they form distinct bundles; the superior ovary is usually trimerous.

Family 1. **Cistaceae.**—Pentamerous, regular flowers, with numerous stamens and three to five carpels united to form a unilocular or multilocular ovary with a single style and parietal placentas. In Britain the Rock Rose (*Helianthemum vulgare*) (Fig. 661). Many species of *Cistus* are characteristic shrubs of the vegetation of the Mediterranean region.

Family 2. **Violaceae.**—Distinguished by dorsiventral flowers with only five stamens. Ovary unilocular with a simple style. The flowers have the anterior petal prolonged backwards as a spur, into which two nectar-secreting processes of the two anterior stamens project (Fig. 662).

Family 3. **Ternstroemiaceae** have a gradual transition from sepals to petals, like that found in the Magnoliaceae, numerous stamens, and a trilocular ovary with axile placentation. The Tea-plant (Fig. 663) and the Camellia belong to this family.

Family 4. **Guttiferae.**—Distinguished by the schizogenous glands and the union in bundles of the stamens. *Hypericum* is a British representative. The red contents of the secretory organs of *Garcinia Hanburyi* when dried form Gamboge.

Family 5. **Dipterocarpaceae.**—Characterised by the great enlargement of some or all the sepals after fertilisation. *Dryobalanops Camphora* yields Borneo Camphor. Dammar is obtained from *Shorea Wiesneri*.

Order 14. Columniferae

The essential character of this order is afforded by the androecium of the regularly pentamerous, actinomorphic, hermaphrodite flowers. One of the two whorls of stamens, usually the outer one, is suppressed or only represented by staminodes, while the other whorl has undergone a greater or less increase in the

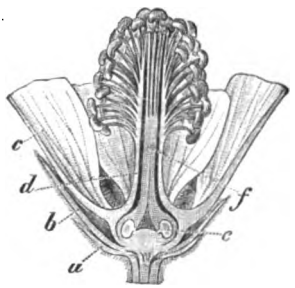


FIG. 664.—Flower of *Althaea officinalis*, cut through longitudinally. *a*, Outer; *b*, inner calyx; *c*, petals; *d*, androecium; *f*, pistil; *e*, ovule. (After BERG and SCHMIDT.)

FIG. 665.—Malvaceae. Floral diagram (*Malva*).

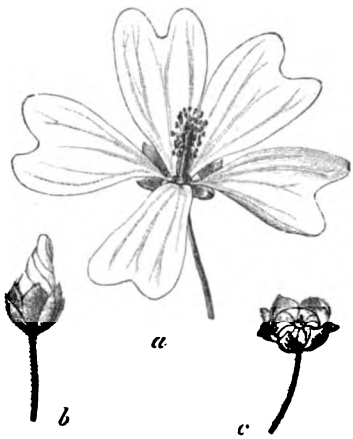


FIG. 666.—*Malva sylvestris*. *a*, Flower; *b*, flower-bud; *c*, fruit. (Nat. size.)

number of its members by chorisis. The branching is frequently accompanied by cohesion of the filaments. The carpels also sometimes exhibit an increase in number as a result of branching. The superior ovary is then divided into a corresponding number of loculi.

Family 1. **Malvaceae.**—Characterised by the flowers with the

Fig. 667.—Flowering branch and open fruit of *Gossypium herbaceum*. (¼ nat. size.) *Official.*

corolla contorted in the bud. Protandrous. Stamens united into a tube around the ovary; the free ends of the stamens, each of which bears a single reniform theca, project from the margin of the staminal tube. K 5, C 5, A∞, G (3) or ∞. Pollen grains with spiny exine, so that they readily adhere to the hairy bodies of insects (Fig. 514).

The genus *Malva* which occurs in Britain includes perennial herbs, with long-stalked, palmately-veined leaves. Flowers solitary or in small cymose inflorescences,

in the axils of leaves. Three free segments of the epicalyx. Petals usually rose-coloured, deeply notched (Fig. 666). In *Althaea* the whole plant is clothed with stellate hairs, giving it a soft velvety appearance. Epicalyx of 6-9 segments united at the base. The fruit is a schizocarp consisting of numerous carpels arranged in a whorl.

Hibiscus and *Gossypium* are shrubs with three- to five-lobed leaves with long stalks. Flowers with a large epicalyx of three segments, which completely covers the calyx. Fruit of three to five carpels, loculicidal. Seed of *Gossypium* covered with long hairs which aid in its dispersion by the wind. When stripped from the seeds and cleaned these hairs form cotton wool. The most important species of Cotton are *G. barbadense*, *G. arboreum*, *G. herbaceum* (Fig. 667).

FIG. 668.—Tiliaceae. Floral diagram (*Tilia*). (After EICHLER.)

FIG. 670.—Sterculiaceae. Floral diagram (*Theobroma*). (After EICHLER.)

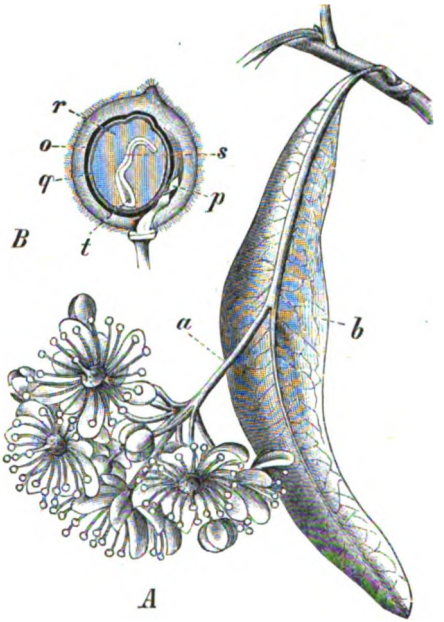


FIG. 669.—*Tilia ulmifolia*. *A*, Inflorescence (*a*), with bract (*b*), (nat. size). *B*, Longitudinal section of fruit (magnified); *o*, pericarp; *p*, atrophied dissepiment and ovules; *q*, seed; *r*, endosperm; *s*, embryo; *t*, its radicle. (After BERG and SCHMIDT.)

OFFICIAL.—*Gossypium barbadense* and other species yield GOSSYPIUM.

Family 2. **Tiliaceae.** — Plants with simple stalked leaves provided with deciduous stipules. Calyx polysepalous. Aestivation of calyx and corolla valvate. Stamens completely free from one another with introrse anthers; usually only the inner whorl is present and has undergone branching (Fig. 668). Style simple.

Most of the genera are tropical. The herbaceous species of *Corchorus* yield Jute. In Britain two species of *Tilia*, Lime, occur. These are stately trees with two-ranked petiolate leaves, the stipules of which are soon shed. The leaves, which have a serrate margin, are asymmetrical. The inflorescence (Fig. 669 *A*) is coherent with a bract for half its length; this serves as a wing in the distribution of the fruit. The umbel-like inflorescence of the Lime is composed of dichasia; *Tilia platyphyllos* has 3-7, *T. parvifolia* 11 or more flowers in the

inflorescence. The hairy ovary has two ovules in each of its five loculi. The fruit only contains one seed (Fig. 669 *B*).

Family 3. **Sterculiaceae.**—This family which is distributed in the tropics resembles the Tiliaceae. Flowers with a gamosepalous calyx ; corolla twisted in

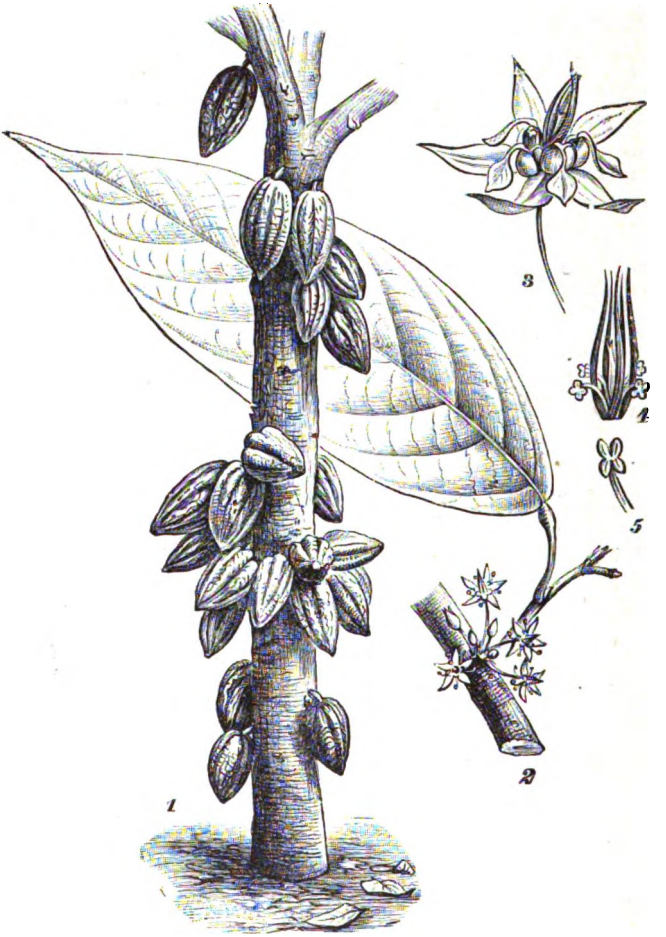


FIG. 671.—*Theobroma Cacao*. *1*, Stem bearing fruits. *2*, Flowering branch. *3*, Flower. *4*, Circle of stamen. *5*, Stamen from anterior side. (*3*, *4*, about nat. size ; *5*, enlarged ; *1*, *2*, greatly reduced.) *OFFICIAL.*

the bud ; stamens coherent to form a tube. The antisepalous stamens are staminodial ; the antipetalous stamens are often increased in number. Anthers extrorse.

The most important plant is the Cocoa tree (*Theobroma Cacao*, Figs. 670, 671). It is a native of tropical Central and South America, but has long been cultivated. It is a low tree with short-stalked, firm, brittle, simple leaves of large size, oval shape, and dark green colour. The young leaves are of a bright red colour, and,

as in many tropical trees, hang limply downwards. The flowers are borne on the main stem or the older branches, and arise from dormant axillary buds (CAULIFLORY). Each petal is bulged out at the base, narrows considerably above this, and ends in an expanded tip. The form of the reddish flowers is thus somewhat urn-shaped with five radiating points. The pentalocular ovary has numerous ovules in each loculus. As the fruit develops, the soft tissue of the septa extends between the single seeds; the ripe fruit is thus unilocular and many-seeded. The seed-coat is filled by the embryo, which has two large, folded, brittle cotyledons. *Cola acuminata* and *C. vera*, natives of tropical Africa, yield the Kola nuts which are used in medicine.

OFFICIAL.—*Theobroma Cacao*, from which OLEUM THEOBROMATIS is obtained.

Orders 15-17 are connected by a number of characters such as reduction in number of stamens, presence of a disc, one-seeded loculi in the fruit; these may indicate a common relationship to the Tricoccae or to the forms from which the latter order came.

Order 15. Gruinales

The flowers of the majority of the plants belonging to this order are hermaphrodite, pentamerous, and radially symmetrical, with a superior, septate ovary. K 5, C 5, A 5 + 5, G (5). When the flowers are zygomorphic they frequently exhibit reduction (Polygalaceae). Stamens coherent at the base, obdiplostemonous

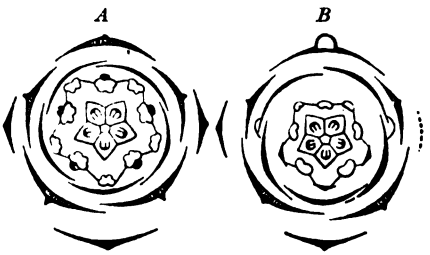


FIG. 672.—Floral diagrams of Geraniaceae. *A*, *Geranium pratense*. *B*, *Pelargonium zonale*. (After EICHLER.)

FIG. 673.—Fruit of *Pelargonium inquinans*. (× 3. After BAILLON.)

or haplostemonous. Nectaries to the outer side of the stamens or as an annular disc within the stamens (Rutaceae). Ovules usually pendulous, with the micropyle directed upwards and the raphe ventral; or the micropyle is downwardly directed and the raphe dorsal.

Family 1. **Geraniaceae.**—The genera *Geranium* with actinomorphic and *Pelargonium* with dorsiventral flowers both have stalked, palmately-veined leaves. Two ovules in each loculus. When ripe the five beaked carpels separate from a central column, and either open to liberate the seeds, or remain closed and by the hygroscopic movements of the awn-like portion bury the seed in the soil (Fig. 673; cf. Fig. 275, p. 334).

Family 2. **Linaceae.**—*Linum usitatissimum*, Flax (Fig. 674), has long been in cultivation. It is an annual, and bears numerous blue flowers, which last only a short time, in racemose cincinni. The flower has its stamens united at the base and five free styles. The stem bears numerous small narrow leaves. The bast-fibres after proper preparation are woven into linen. The seeds from the 5-locular capsule yield oil.

OFFICIAL.—LINUM, the seeds of *Linum usitatissimum*.

Family 3. **Erythroxylaceae.**—*Erthroxylon Coca* is a small Peruvian shrub, with entire, simple leaves and axillary groups of small white flowers (Fig. 675). Cocaine is obtained from the leaves of this plant.

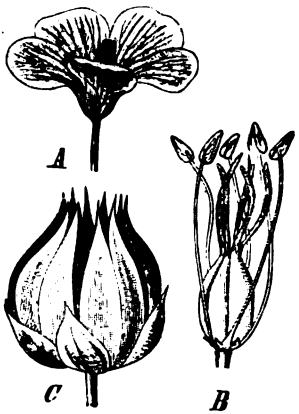


FIG. 674.—*Linum usitatissimum*. *A*, Flower. *B*, Androecium and gynaeceum. *C*, Capsule after dehiscence. (*A*, nat. size; *B*, *C* ×3.) *OFFICIAL.*

FIG. 675.—*Erythroxylon Coca*. (⅓ nat. size.)

Family 4. **Zygophyllaceae.**

OFFICIAL.—*Guiacum sanctum* and *Guiacum officinale*, West Indian trees with opposite, paripinnate leaves. Ovary bicarpellary, bilocular. Fruit winged. They yield GUIACI LIGNUM and GUIACI RESINA.

Family 5. **Rutaceae.**—IMPORTANT GENERA.—*Ruta graveolens* (Fig. 676), the Rue, is a somewhat shrubby plant with pinnately-divided leaves. The terminal flowers of the dichasial inflorescences are pentamerous in robust examples; all the other flowers are tetramerous with a large intrastaminal disc. *Dictamnus Fraxinella* has panicles of conspicuous, dorsiventral flowers; the carpels are free in their upper portions. The important genus *Citrus* (22) has peculiarly constructed flowers (Figs. 677, 678). The numerous stamens are united in bundles

and arranged in a single whorl. The number of carpels is also increased. The fruit is a berry; the succulent portion is formed of large cells with abundant cell-sap which project into and fill up the loculi of the ovary. The seeds have usually several embryos (cf. p. 578). The leaves of many species are simple and provided with more or less winged petioles. Other species have trifoliate leaves, and the articulation at the base of the lamina shows that the apparently simple leaves correspond to imparipinnate leaves, of which only the terminal leaflet is developed. The thorns at the base of the leaf are derived by modification of the first leaves of the axillary bud.

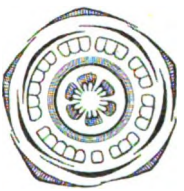


FIG. 677.—Floral diagram of *Citrus vulgaris*. (After EICHLER.)

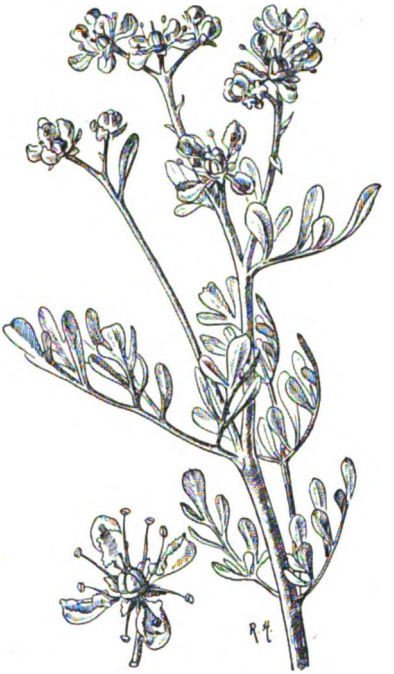


FIG. 676.—*Ruta graveolens*. (½ nat. size.)

Citrus is originally an East Asiatic genus; a number of species inhabit the warmer valleys of the Himalayas. All the important cultivated forms have been obtained from the Chinese. *Citrus decumana*, the Shaddock, is tropical; *C. medica* is the form which was known to the Greeks in the expeditions of Alexander as the Median apple. It is now widely spread and has a number of varieties of which *Citrus* (*medica*) *Limonum* is the Lemon. This tree was introduced into the Mediterranean region in the third or fourth century. *Citrus* (*medica*)

FIG. 678.—*Citrus vulgaris*. (½ nat. size.) *OFFICIAL.*

Bajoura has thick-skinned fruits from which citron is obtained. *Citrus Aurantium* occurs in two distinct forms, *C.* (*Aurantium*) *vulgaris* (Fig. 678) and *C.* (*Aurantium*) *sinensis*. *Citrus nobilis*, the Mandarin, is also of Chinese origin. Chimaeras, called *Bizzaria*, have been obtained by grafting between *Citrus Aurantium* and *C. Limonum*. *Pilocarpus jaborandi*, a tree-like shrub with large, imparipinnate leaves, native of Eastern Brazil.

FIG. 679.—*Quassia amara*. (Nat. size. After BERG and SCHMIDT.)

OFFICIAL.—*Citrus Aurantium*, var. *Bigaradia*, yields AURANTII CORTEX SICCATUS, AURANTII CORTEX RECENS, and AQUA AURANTII FLORIS. *Citrus medica*, var. *limonum*, gives LIMONIS CORTEX, and LIMONIS SUCCUS. *Aegle marmelos* yields BELAE FRUCTUS. BUCHU FOLIA are obtained from *Barosma betulina*.

Family 6. **Simarubaceae**. — Contain bitter principles. *Quassia amara* (Surinam) (Fig. 679), a small tree with beautiful leaves and showy flowers.

OFFICIAL.—QUASSIAE LIGNUM from *Picrasma excelsa* (West Indies).

Family 7. **Burseraceae.**—Woody plants with resin passages. *Commiphora abyssinica* and *C. Schimperi* are trees found in Arabian East Africa. *Boswellia Carteri* and *B. Bhau Dajianae* are small trees from the same region which yield OLIBANUM. *Canarium.*

OFFICIAL. —MYRRHA, Myrrh, from *Balsamodendron Myrrha* and other species.

Family 8. **Polygalaceae.**—K 5, C 3, A (8), G (2). The two lateral sepals are petaloid. Three petals, the lowest of which forms a keel. Stamens 8, coherent into a tube (Figs. 680-682). *Polygala chamaebuxus* is a small shrubby plant occurring in the Alps. *P. vulgaris* and *P. amara* occur in Britain.

OFFICIAL.—*Polygala Senega* (North America) yields SENEGAE RADIX.

Order 16. Sapindinae

This includes the following families:—

Family 1. **Sapindaceae.**—Tropical. The crushed seeds of *Paullinia cupana*, a liane of Brazil, yield GUARANA.

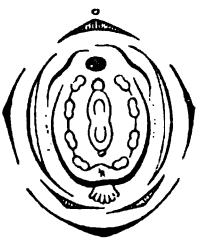


FIG. 680.—Floral diagram of *Polygala myrtifolia.* (After EICHLER.)

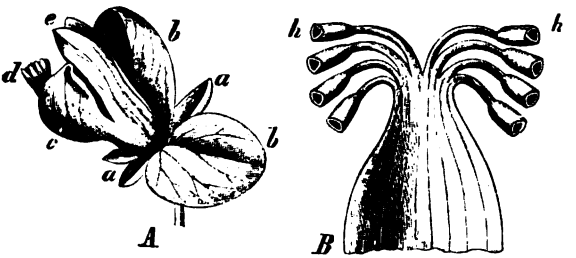


FIG. 681.—*Polygala Senega.* *A*, Flower; *a*, small; *b*, large sepals; *c*, keel; *e*, lateral petals; *d*, androecium. *B*, Androecium; *h*, anthers (magnified). (After BERG and SCHMIDT.) *OFFICIAL.*

FIG. 682.—*Polygala Senega.* (½ nat. size.) *OFFICIAL.*

Family 2. **Anacardiaceae.**—Mostly tropical. *Mangifera indica*; *Rhus toxicodendron*; *Pistacia.*

Family 3. **Aquifoliaceae.**—*Ilex aquifolium.* The Holly, an evergreen shrub or tree of Western Europe (Fig. 683). *I. paraguariensis* yields Paraguay Tea or Maté.

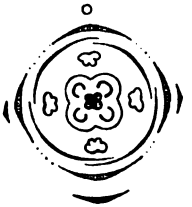


FIG. 683.—Floral diagram of *Ilex aquifolium*.
(After EICHLER.)

FIG. 684.—*Acer pseudoplatanus* (½ nat. size). *1*, Branch with pendulous terminal inflorescence. *2*, Male flower. *3*, Female flower. *4*, Fruit. *5*, Floral diagram. (*2* and *3* enlarged.) (After EICHLER.)

Family 4. **Aceraceae.**—Include Maples and Sycamores with their characteristically winged fruits (Fig. 684).

Family 5. **Hippocastanaceae.**—The Horse-chestnut. *Aesculus hippocastanum.*

Order 17. Frangulinae

This order is characterised by the single whorl of antipetalous stamens and the intrastaminal disc.

Family 1. **Rhamnaceae.**—The only native genus of this family, which is distributed in the tropics, is *Rhamnus.*

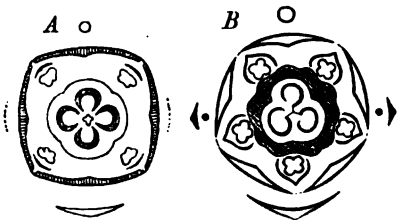


FIG. 685.—Floral diagrams of *A*, *Rhamnus cathartica* (represented as hermaphrodite), and *B*, *Rh. Frangula.* (After EICHLER.)

Rh. Frangula (Figs. 685 *B*, 686, 687), the Berry-bearing Alder, is a shrub with alternate, entire leaves provided with small stipules. The flowers are solitary or in groups in the axils of the leaves; pentamerous, with two carpels. The floral receptacle forms a cup-shaped disc. Two (less commonly three) carpels; stigma undivided. Fruit, a drupe with two or three seeds. *Rh. catharticus* has usually spiny branches bearing opposite leaves with serrate margins. Flowers tetramerous throughout (Fig. 685 *A*), dioecious by suppression of stamens or carpels; female flower with four free styles and a four-seeded drupe. Seeds with a dorsal raphe. *Colletia spinosa*

FIG. 686.—*Rhamnus Frangula* (½ nat. size). Flowering branch and portion of a branch bearing fruits.

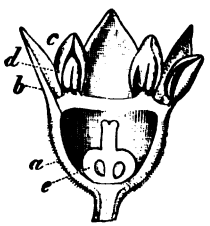


FIG. 687.—*Rhamnus Frangula.* Flower cut through longitudinally. *a*, Receptacle; *b*, calyx; *c*, petal; *d*, a stamen; *e*, pistil (magnified). (After BERG and SCHMIDT.)

and *C. cruciata* are leafless South American shrubs; the thorns of the former are cylindrical, those of the latter flattened laterally.

OFFICIAL. — *Rhamnus purshianus* yields CASCARA SAGRADA or RHAMNI PURSHIANI CORTEX.

Family 2. **Vitaceae** (Figs. 688, 689).—The genera *Vitis*, *Ampelopsis*, and *Parthenocissus* in the northern hemisphere and the tropical genus *Cissus* belong here. *Vitis vinifera*, the Grape Vine, is a cultivated plant with numerous races and varieties. The tendrils correspond to shoots and stand opposite to the leaves; they are at first terminal, but become displaced to one side by the development of the axillary shoot. The inflorescence is a panicle taking the place of a tendril; intermediate forms between inflorescences and tendrils are of frequent occurrence. Calyx only represented by a small rim; the pentamerous corolla, with the petals united by their tips, is thrown off when the flower opens. Raisins are obtained from *Vitis vinifera*. Currants are the seedless fruits of *Vitis vinifera*,

FIG. 688.—*Vitis vinifera*. Opening flower. *a*, Calyx; *b*, corolla; *c*, disc; *d*, stamens; *e*, ovary (magnified). (After BERG and SCHMIDT.)

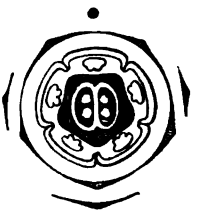


FIG. 689.—Floral diagram of *Ampelopsis hederacea*. (After EICHLER.)

var. *apyrena*. Species of *Parthenocissus* distributed in North America and Asia go by the name of Wild Vines; some of them have tendrils with adhesive discs (Fig. 210).

Order 18. Rosiflorae

The cyclic flowers are in other respects similar to those of the Polycarpicae; the connection of the Rosaceae with the Calycanthaceae is particularly close. The single carpel in the Pruneae and the dorsiventral flowers of the Chrysobalaneae lead on to the Leguminosae.

The order includes plants of very diverse form and construction with alternate leaves. The flowers are almost always actinomorphic with the members arranged in whorls; they have five, ten or numerous stamens and carpels, the pistil is as a rule apocarpous. The large part played by the floral axis in the construction of the flower and fruit is characteristic. K5, C5, A5–∞, G1–∞.

Family 1. **Crassulaceae.**—Succulent herbs (cf. p. 174) or under-shrubs with cymose inflorescences. *Sedum* (Fig. 690) with pentamerous flowers; there are a number of British species. *Sempervivum*, flowers with from six to an indefinite number of members in the whorls; *S. tectorum*. *Bryophyllum* with tetramerous flowers, noteworthy on account of the abundant formation of buds in the indentations of the margin of the leaf. *Crassula*; South African forms mimic stones by their globular form (23).

Family 2. **Saxifragaceae.**—Herbs or woody plants with hermaphrodite, obdiplostemonous flowers. Fruit a capsule or a berry formed of two carpels and containing an indefinite number of albuminous seeds. *Saxifraga*, Saxifrage, small herbaceous plants which are especially numerous on crags and rocky ground in

FIG. 690.—*Sedum Telephium*. *a*, Flower; *b*, flower in longitudinal section. (× 4. After H. SCHENCK.)

mountainous districts. They have a rosette of radical leaves and bear numerous pentamerous flowers grouped in various types of inflorescence. The two partially inferior carpels are distinct from one another above. *Parnassia palustris* is common on wet moors, pentamerous flower with 4 carpels. One whorl of stamens modified

FIG. 691.—*Ribes rubrum*. (⅓ nat. size.)

into palmately-divided staminodes, which serve as nectaries. The species of *Ribes* have an inferior ovary which develops into a berry, and on this account are commonly cultivated. *R. rubrum* (Fig. 691), Red Currant, *R. nigrum*, Black Currant, *R. grossularia*, Gooseberry. Other Saxifragaceae are favourite ornamental plants, *e.g. Ribes aureum* and *R. sanguineum*, *Hydrangea*, *Philadelphus*, and *Deutzia*.

Family 3. **Rosaceae** ([24]).—Characteristic features of this family are the constant presence of stipules, the absence of endosperm from most of the seeds, the apocarpous fruits, and, as a rule, the numerous stamens (Fig. 692). The two latter features are also found in the Ranunculaceae, or generally in the Polycarpicae, but the floral members are there spirally arranged while in the Rosaceae they are in whorls, and the flowers are perigynous.

In many cases the increase in number of members of the androecium and gynaeceum proceeds from an intercalary zone of the hollowed floral axis, and continues for a considerable period. The introduction of new members is determined by the spatial relations, so that differences in the numbers of members are found in individuals of the same species.

The genus *Spiraea* has typically pentamerous flowers with superior ovaries; many species are cultivated as ornamental shrubs (Fig. 692 *E*). *Quillaja Saponaria* (Fig. 693), from Chili, is an evergreen tree with shortly-stalked, alternate,

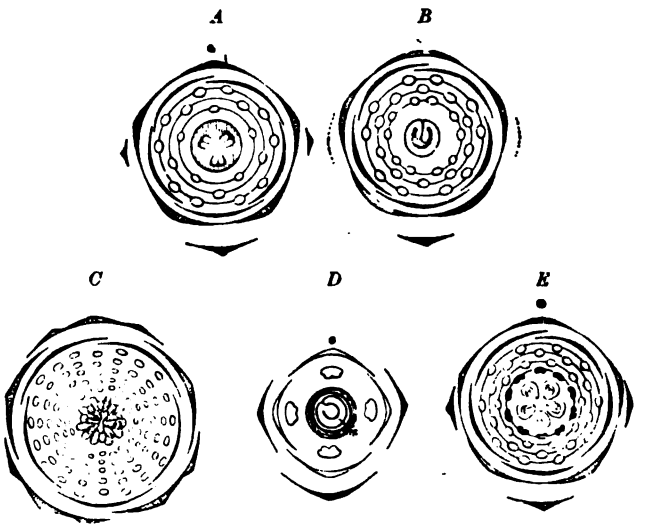


FIG. 692.—Floral diagrams of Rosaceae. *A*, *Sorbus domestica*. *B*, *Prunus Padus*. *C*, *Rosa tomentosa*. *D*, *Sanguisorba officinalis*. *E*, *Spiraea hypericifolia*. (After EICHLER.)

leathery leaves and terminal dichasia usually consisting of three flowers. The flower has a five-toothed, nectar-secreting disc projecting above the large sepals. Five of the stamens stand at the projecting angles of the disc opposite the sepals; the other five are inserted opposite the petals at the inner margin of the disc. Petals narrow, white. Ovary superior. Only the middle flower of the dichasium is hermaphrodite and fertile, the lateral flowers are male and have a reduced gynaeceum. Fruit star-shaped, composed of partial fruits. Each carpel dehisces by splitting into two valves. Seeds winged.

The genera *Pyrus*, *Cydonia*, etc., are distinguished from the other Rosaceae by their inferior ovary, which usually consists of five carpels bound together by the

hollow floral receptacle so that only the styles are free. The fruit resembles a berry, the floral receptacle becoming succulent. The boundaries of the separate loculi are formed of parchment-like or stony tissue. *Pyrus malus*, Apple (Fig. 521, 3; Fig. 694), and *P. communis*, the Pear, are important and long-cultivated fruit trees, of which numerous varieties are grown. *Cydonia vulgaris*, the Quince, has large, solitary, rose-coloured flowers. The fruits are in shape like an apple or pear, covered with fine woolly hairs and with a pleasant scent, though not edible when uncooked. In *Mespilus germanica*, the Medlar, the fruit has an apical depression surrounded by the remains of the calyx. The evergreen *Eriobotrya japonica*, is commonly planted in the Mediterranean region; *Sorbus*

FIG. 693.—*Quillaja Saponaria*. (¼ nat. size. After A. MEYER and SCHUMANN.)

FIG. 694.—*Pyrus malus*. Flowering shoot, single flower, and fruit in longitudinal section. (½ nat. size.)

(*Pyrus*) *aucuparia*, the Rowan. *Crataegus* (*Mespilus*) *oxycantha*, the Hawthorn, in hedges or planted as an ornamental tree (cf. p. 318).

A concave, pitcher-shaped floral axis with one to many free carpels, each of which encloses 1-2 ovules, characterises the genus *Rosa*. The partial fruits are nut-like, and are enclosed by the hollowed floral axis (Figs. 569, 692 *C*). The leafy development of the numerous stamens has given rise to the cultivated double forms. *Agrimonia* and *Hagenia abyssinica* have a dry cup-shaped receptacle. *Hagenia* is a dioecious tree with unequally pinnate leaves, the adherent stipules of which render the petiole winged and channelled. Inflorescence a copiously branched panicle. Each flower has two bracteoles and an epicalyx. The flowers are unisexual by suppression of the male and female organs respectively. The corolla later falls off and the sepals become inrolled, while the epicalyx enlarges. The two free carpels have each a single ovule. Fruit one-seeded (Figs. 695, 696). *Alchemilla* has no petals (Fig. 521, 2). *Sanguisorba officinalis* has polygamous

flowers, without epicalyx or corolla, aggregated in heads. Flowers tetramerous with 1-2 carpels (Fig. 692 *D*). These are greatly reduced forms.

FIG. 695.—*Hagenia abyssinica*. *1*, Female flower; *e*, epicalyx; *f*, calyx; *g*, corolla (× 4). *2*, Fruit (nat. size), with enlarged epicalyx. (After BERG and SCHMIDT.) *OFFICIAL.*

FIG. 696.—*Hagenia abyssinica*. Inflorescence (¼ nat. size). (After BERG and SCHMIDT.) *OFFICIAL.*

Potentilla with a number of British species has a flattened receptacle, epicalyx, and an apocarpous pistil. *Geum* and *Dryas* have hairy carpels which elongate in fruit and are distributed by the wind. *Fragraria*, Strawberry, with small achenes situated on the succulent, enlarged, floral receptacle. *Rubus*, Blackberry, has numerous species, mostly scrambling shrubs with recurved prickles. Leaves

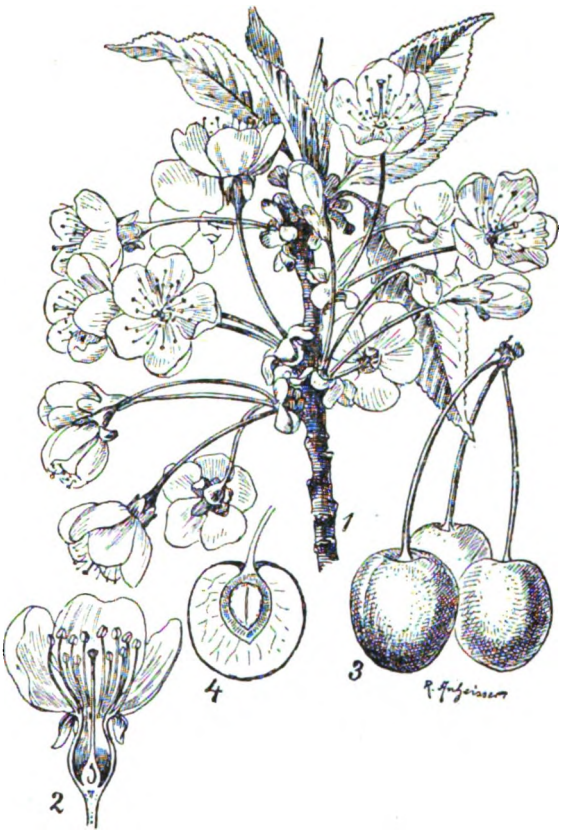


FIG. 697.—*Prunus cerasus* (⅓ nat. size). *1*, Flowering shoot; *2*, flower cut in two (slightly enlarged); *3*, fruits; *4*, fruit cut through longitudinally.

trifoliate. *R. idaeus*, the Raspberry, is one of the few species which are not straggling climbers. The small drupes are closely crowded on the convex receptacle, forming the collective fruit.

The group of the Pruneae which includes a number of important trees bearing stone-fruits has a single carpel situated in the middle of the flat expanded floral receptacle (Fig. 692 *B*). *Prunus cerasus*, the Wild Cherry (Fig. 697); *P. avium*, Gean; *P. domestica*, the Plum; *P. armeniaca*, the Apricot, and *P. persica*, the Peach, are of Chinese origin; *P. Amygdalus*, the Almond, from the eastern Mediterranean region. The succulent mesocarp of the Almond dries up as the fruit ripens and ruptures, setting the stony endocarp free.

Poisonous.—The seeds of many Rosaceae contain amygdalin, but usually not in such amount as to be poisonous, owing to the resulting hydrocyanic acid, when eaten fresh in small quantity; this is, however, often the case with the residuum left after the seeds, *e.g.* of bitter almonds, have been crushed. The leaves of the Cherry Laurel (*Prunus laurocerasus*) may also give rise to toxic effects.

Official.—Rosae gallicae petala from cultivated plants of *Rosa gallica*; oleum rosae and aqua rosae from *Rosa damascena*. Amygdala dulcis and amygdala amara from *Prunus amygdalus*. Prunum from *Prunus domesticus*. Pruni virginianae cortex from *Prunus serotina*. Laurocerasi folia from *Prunus laurocerasus*. Cusso from *Hagenia abyssinica*. Quillaiae cortex from *Quillaja Saponaria*.

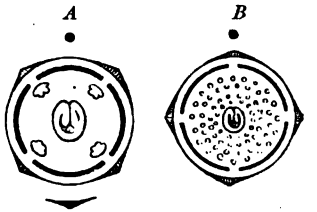


Fig. 698.—Floral diagrams of Mimosaceae. *A*, *Mimosa pudica*. *B*, *Acacia lophantha*. (After Eichler.)

Order 19. Leguminosae

The common characteristic of all Leguminosae is afforded by the pistil. This is always formed of a single carpel, the ventral suture of which is directed to the dorsal side of the flower (Figs. 698, 701, 706). It is unilocular, and bears the ovules in one or two rows on the ventral suture. The fruit is usually a pod (legume), which dehisces by splitting along both the ventral and dorsal sutures (Fig. 711). Nearly all Leguminosae have

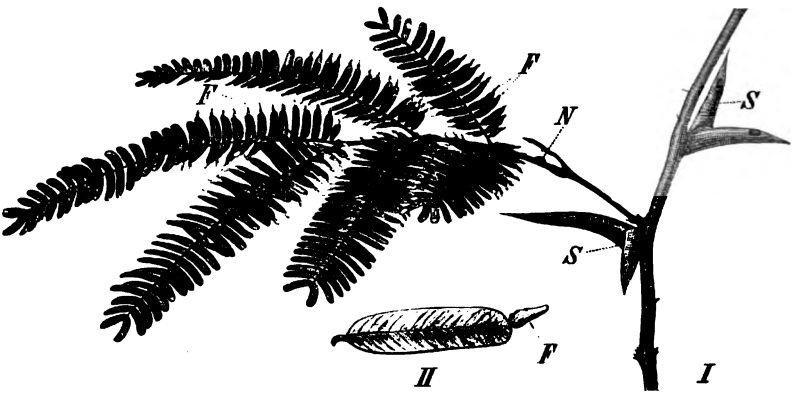


Fig. 699.—*Acacia nicoyensis*. From Costa Rica. *I*, Leaf and part of stem; *S*, hollow thorns in which the ants live; *F*, food bodies at the apices of the lower pinnules; *N*, nectary on the petiole. (Reduced.) *II*, Single pinnule with food-body, *F*. (After F. Noll. Somewhat enlarged.)

alternate, compound, stipulate leaves. Many are provided with pulvini (Figs. 132, 290, 291), which effect variation movements of the leaves and leaflets.

Family 1. **Mimosaceae.**—Trees, and erect, or climbing, shrubby plants with bipinnate leaves. Flowers actinomorphic, pentamerous or

tetramerous (Fig. 698). Aestivation of sepals and petals valvate. Stamens free, numerous, or equal or double in number to the petals.

FIG. 700.—*Acacia catechu*. (⅓ nat. size. After MEYER and SCHUMANN.) *OFFICIAL.*

The colour of the flower is due to the length and number of the stamens, the corolla being as a rule inconspicuous. The pollen grains are often united in tetrads or in larger numbers. The flowers are grouped in spikes or heads. Embryo straight in the seed.

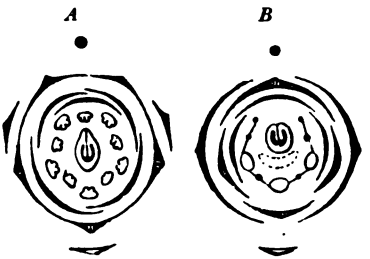


FIG. 701.—Floral diagrams of Caesalpiniaceae. *A*, *Cercis siliquastrum*. *B*, *Tamarindus indica*. (After EICHLER.)

FIG. 702. *Cassia angustifolia*. (⅓ nat. size. After A. MEYER and SCHUMANN.) *OFFICIAL.*

There are no representatives native to Europe of this family, which is abundant in the tropics. The Sensitive Plant (*Mimosa pudica*) (Fig. 291) occurs as a weed throughout the tropics and exhibits great irritability to contact. Numerous species of the genus *Acacia* are distributed through the tropics and sub-tropics of the Old and New Worlds; some are in cultivation in the Mediterranean region. The Australian forms of the genus are frequently

FIG. 703.—*Tamarindus indica*. (½ nat. size. After A. MEYER and SCHUMANN.) *OFFICIAL.*

characterised by possessing phyllodes (Figs. 136, 192), the vertical position of which contributes to the peculiar habit of the Australian forests. Some American species of *Acacia* are inhabited by ants (Fig. 699) which live in the large stipular thorns and obtain food from Belt's food-bodies ([25]) at the tips of the pinnules. A mutual symbiosis has not been demonstrated in this case. Many species of *Acacia* are of considerable economic value owing to the presence of gums and tannins in the cortex or in the heart-wood. *A. catechu* (Fig. 700) and *A. suma* are East Indian trees from which Catechu is obtained.

OFFICIAL.—By the disorganisation of the parenchyma of the stem of *Acacia*

senegal (Soudan and Senegambia) and of other species, ACACIAE GUMMI is obtained. This exudes from wounds as a thick fluid and hardens in the air. *A. arabica*, *A. catechu* and *A. decurrens* are also official.

Family 2. **Caesalpiniaceae.**—Trees or shrubs with pinnate or bipinnate leaves. Flowers usually somewhat dorsiventral. Corolla

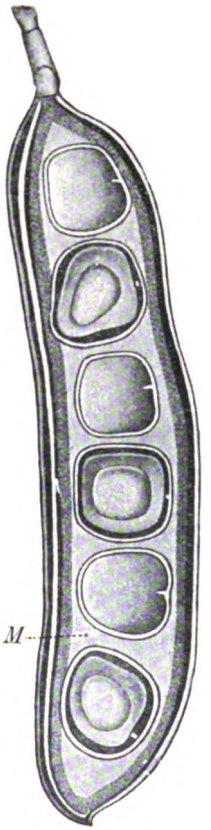


FIG. 704. — *Tamarindus indica*. Fruit in longitudinal section. *M*, the fleshy mesocarp. (After BERG and SCHMIDT.) *OFFICIAL.*

FIG. 705.—*Krameria triandra*. (½ nat. size. After A. MEYER and SCHUMANN.) *OFFICIAL.*

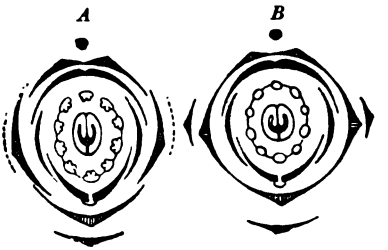


FIG. 706.—Floral diagrams of Papilionaceae. *A*, *Vicia Faba*. *B*, *Laburnum vulgare*. (After EICHLER.)

with ascending imbricate aestivation (Fig. 701) or wanting. Typical floral formula: K 5, C 5, A 5 + 5, G $\underline{1}$. The number of petals and stamens is often incomplete. Embryo straight.

Abundantly represented in the tropics and sub-tropics.

In *Cassia angustifolia* the sepals and petals are both five in number and free

(Fig. 702). The lower overlapping petals are somewhat larger than the upper ones. Of the ten stamens the three upper ones are short and sterile, while the other seven, the filaments of which are curved and convex below, diminish in length from above downwards. The anthers open by means of terminal pores. The pod is compressed and broad and flat. The flowers are borne in racemes in the axils of the leaves of the shrub, which is about a metre high. The bright green, equally pinnate leaves have small stipules at the base. *Tamarindus indica* (Fig. 703) is a handsome tree, native to tropical Africa, but now planted throughout the tropics. Its broadly-spreading crown of light foliage makes it a favourite

FIG. 707.—*Lotus corniculatus* (½ nat. size). Flowering shoot; flower, keel, stamens. Carpel (nat. size) and fruit (½ nat. size).

FIG. 708.—*Myroxylon Pereirae*. (⅓ nat. size. After BERG and SCHMIDT.) *OFFICIAL.*

shade-tree. The racemes of flowers are terminal on lateral twigs bearing equally pinnate leaves. The individual flowers are markedly zygomorphic. The fruit is peculiar. The pericarp is differentiated into an outer brittle exocarp, a succulent mesocarp, and a firm endocarp consisting of stone-cells investing the more or less numerous seeds individually (Fig. 704). The almost imperceptibly dorsiventral flowers of *Copaifera* have no corolla; the four sepals are succeeded by 8-10 free stamens. The fruit is one-seeded but opens when ripe. The seed is invested on

one side by a succulent, irregularly-limited arillus. None of the Caesalpiniaceae are British. *Ceratonia siliqua* and the cauliflorous (cf. p. 651) *Cercis siliquastrum* from the Mediterranean region (Fig. 701 *A*) and *Gleditschia triacanthos* (N. Am.) (Fig. 199), are sometimes cultivated as ornamental plants.

OFFICIAL.—SENNA INDICA, the pinnae of *Cassia angustifolia* (Trop. East Africa and Arabia, cultivated at Tinnevelly in Southern India); SENNA ALEXANDRINA from *C. acutifolia*; *Cassia fistula* (Trop. Am.) yields CASSIAE PULPA; COPAIBA is obtained from *Copaifera Langsdorfii* and other species; TAMARINDUS from the succulent mesocarp of *Tamarindus indica*; HAEMATOXYLI LIGNUM, the heart-wood of *Haematoxylon campechianum* (Trop. Am.); KRAMERIAE RADIX from *Krameria triandra*, a shrub growing in the Cordilleras. Flowers atypical; the sepals brightly coloured within; the corolla small. Three stamens opening by pores at the summit. Fruit spherical, prickly. Leaves simple, silvery white (Fig. 705).

Family 3. **Papilionaceae.**—Herbs, shrubs, or trees with, as a rule, imparipinnate leaves. Flowers always markedly zygomorphic.

FIG. 709.—*Myroxylon Pereirae*. See Text. (Enlarged. After BERG and SCHMIDT.) *OFFICIAL.*

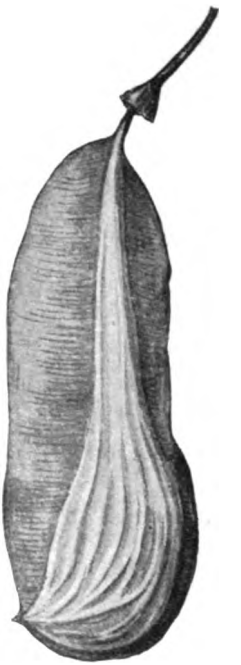


FIG. 710.—Fruit of *Myroxylon Pereirae*. (⅓ nat. size.) *OFFICIAL.*

Calyx of five sepals. Corolla of five petals, papilionaceous, with descending imbricate aestivation (Fig. 706). Stamens 10; filaments either all coherent into a tube surrounding the pistil (*Lupinus*) or the posterior stamen is free (*Lotus*), or all are free (*Myroxylon*, Fig. 709). Seeds with a curved embryo.

Abundantly represented in the temperate zones; fewer in the tropics.

The component parts of a papilionaceous flower are seen separately in Fig. 707. The posterior petal, which overlaps the others in the bud (Fig. 706), is termed the standard (vexillum). The two adjoining lateral petals are the wings (alae), and the two lowest petals, usually coherent by their lower margins, together form the keel

(carina). The upper ends of the stamens are usually free and curve upwards, as does also the style bearing the stigma.

The genus *Myroxylon* is of importance on account of the balsam obtained from species belonging to it. *Myroxylon Pereirae* is a tree of moderate height with alternate, imparipinnate leaves (Fig. 708). The flowers are borne in the terminal racemes and have a large vexillum, the other petals remaining narrow and incon-

FIG. 711.—*Laburnum vulgare.* (½ nat. size.) *POISONOUS.*

spicuous. The stamens are only coherent at the base, and bear conspicuous, reddish-yellow anthers (Fig. 709). The fruit is very peculiar. The ovary has a long stalk and bears two ovules near the tip. One of these develops into the seed of the indehiscent, compressed pod, which has a broad wing along the ventral suture and a narrower wing along the dorsal suture (Fig. 710). The bell-shaped calyx persists on the stalk. *Genista*, *Sarothamnus*, *Lupinus*, *Cytisus* have all ten stamens united (Fig. 706 *B*); their leaves are pinnate or simple, with entire margins. The Laburnum (*Laburnum vulgare*, Fig. 711) is one of the commonest ornamental trees of our gardens and grows wild in the Alps. It has

tripinnate leaves and long pendulous racemes of yellow flowers. *Ulex*, Furze, a characteristic British plant. *Spartium*, distributed in the Mediterranean region. *Trifolium*, Clover, with persistent calyx and corolla. Leaves trifoliate. Flowers aggregated in heads. Stamens (9)+1. Fruits indehiscent. *Medicago*, Medick, with deciduous corolla; fruit sickle-shaped or spirally twisted. *Melilotus*, Melilot, with racemose inflorescences. *Trigonella* with long pods. *Ononis*, Rest-Harrow with ten coherent stamens. The increase in the amount of nitrogen in the soil effected by the root-tubercles (cf. p. 260, Figs. 251, 252) of Leguminosae finds its practical application in European agriculture in the cultivation of species of *Trifolium*, *Medicago*, and *Lupinus*. *Lotus*, Bird's-foot Trefoil (Fig. 707); leaves imparipinnate, lowest pair of leaflets owing to the absence of the petiole resembling stipules. *Anthyllis*, Kidney-Vetch. In species of *Astragalus*, which are low shrubs of the eastern Mediterranean region and of western Asia, the rachis of the leaf persists as a sharply pointed thorn for years after the leaflets have fallen. These spines serve to protect the young shoots, leaves, and flowers (Fig. 712). Our native species are herbaceous. *Robinia* (Fig. 198) is an American tree of rapid growth with very brittle wood, which is often planted and known as False Acacia. *Glycyrrhiza*, Liquorice, is a native of S. Europe. *Wistaria sinensis* is a climber with beautiful blue flowers, often grown against the walls of houses. Distinguished by the jointed pods in which the seeds are isolated by transverse septa are *Coronilla* (Fig. 713), *Ornithopus sativus*, Bird's-Foot, and *Arachis hypogaea*, Ground-nut, an important, oil-yielding fruit of the tropics and sub-tropics. After flowering the flower-stalks penetrate the soil in which the fruits ripen. *Vicia*, Vetch; *Pisum*, Pea (Fig. 208); *Lens*, Lentil; *Lathyrus*, Everlasting Pea (Fig. 209). Leaves with terminal tendrils, corresponding to the terminal leaflet; the leaves may thus appear to be paripinnate. The cotyledons remain within the seed-coat

FIG. 712.—*Astragalus gummifer*. (½ nat. size. After A. MEYER and SCHUMANN.) *OFFICIAL*.

and do not become green. *Vicia Faba*, the Broad Bean, is an erect plant, without tendrils; the terminal leaflet is reduced to a bristle-shaped stump. *Phaseolus*, Kidney Bean, and *Physostigma* are twining plants with tripinnate leaves. *Physostigma venosum*, a West African climber, yields Calabar Bean.

Poisonous. — Among our common Leguminosae only *Laburnum vulgare* and the related genus *Cytisus* are extremely poisonous. *Coronilla varia* (Fig. 713), with umbels of rose-coloured flowers, and *Wistaria sinensis* are also poisonous.

Official.—*Astragalus gummifer* and other species yield TRAGACANTHA. GLYCYRRHIZAE RADIX is obtained from *Glycyrrhiza glabra*. *Spartium scoparium* yields SCOPARII CACUMINA. *Andira araroba*, a Brazilian tree, contains a powdery excretion in cavities of the stem called ARAROBA; CHRYSAROBINUM is obtained from this. The heart-wood of *Pterocarpus santalinus*, an East Indian tree, is PTEROCARPI LIGNUM. KINO is obtained from the juice flowing from incisions in the trunk of *Pterocarpus marsupium*. *Myroxylon toluifera* (S. America) yields BALSAMUM TOLUTANUM, and *M. Pereirae* (San Salvador) BALSAMUM PERUVIANUM. *Arachis hypogaea* yields OLEUM ARACHIS. *Butea frondosa* yields BUTEAE GUMMI.

Fig. 713.—*Coronilla varia* (nat. size). *Poisonous.*

Order 20. Myrtiflorae

This order differs from the Rosiflorae by the inferior ovary and the absence of stipules.

Family 1. **Thymelaeaceae.**—Ovule pendulous. *Daphne Mezereum* (Fig. 714) is a poisonous shrub, possibly native to Britain, which flowers in February and March before the leaves appear. The flowers are rose-coloured, scented, tetramerous, and have no corolla. The leaves form a close tuft until the axis elongates. The fruit is a bright red berry. In the Alps and in the Mediterranean region there are several species of *Daphne*, all of which are poisonous.

Official.—*Daphne Mezereum*, *D. Laureola*, and *D. Gnidium* yield MEZEREI CORTEX.

Family 2. **Elaeagnaceae.**—Ovule erect. *Hippophaë*. *Elaeagnus*. The leaves and young twigs are covered with shining peltate hairs.

Family 3. **Lythraceae.**—*Lythrum salicaria*. Purple Loosestrife. Flowers

typically hexamerous with two inferior carpels. Heterostyled with three forms of flower (cf. p. 560).

Family 4. **Onagraceae.**—Flower tetramerous throughout. Androecium obdiplostemonous. *Epilobium*, Willow-herb, with numerous species; the fruit is a capsule, and the seeds have hairs serving for wind-dispersal. *Oenothera* (Fig. 715). The power of mutating possessed by plants of this genus was recognised by DE VRIES and forms the experimental basis of his hypothesis of mutation. *Circaea*, Enchanter's Nightshade. *Trapa*, Water Nut. Many forms are in cultivation, for instance the species of *Fuchsia*, in which the calyx is petaloid. These plants are natives of America. Fruit a berry.

FIG. 714.—*Daphne Mezereum* (½ nat. size). *OFFICIAL* and *POISONOUS*.

Family 5. **Rhizophoraceae.**—Plants occurring in the Mangrove formation along tropical coasts, characterised by vivipary and the possession of stilt-roots, or respiratory roots (Fig. 189). These adaptations are related to the peculiarities of the situations in which the trees grow. *Rhizophora* (Fig. 716); *Bruguiera*; *Ceriops*. *Kandelia* (Fig. 581). All occur on the coasts of the Indian Ocean. Species of *Rhizophora* are more widely distributed on tropical coasts.

FIG. 715.—Floral diagram of *Oenothera* (Onagraceae). After NOLL.

Family 6. **Myrtaceae.**—Evergreen shrubs or trees; leaves opposite, leathery, often aromatic. Flowers actinomorphic, tetramerous or pentamerous. Androecium of many stamens, which are often arranged in bundles which have originated by branching. Carpels two or many (Fig. 717) united with the floral axis to form the inferior ovary. Fruit, usually a berry or a capsule.

Mainly distributed in tropical America and in Australia.

The Myrtle (*Myrtus communis*), which occurs in the Mediterranean region, is

the only European species. Species of *Eucalyptus* (26) from Australia, especially *E. globulus*, are commonly planted in Italy, on account of their rapid growth and useful timber. Young plants have opposite, sessile leaves, but older trees bear stalked, sickle-shaped leaves which hang vertically. The shadeless condition of the Australian forests formed by these trees depends in part on this character, but

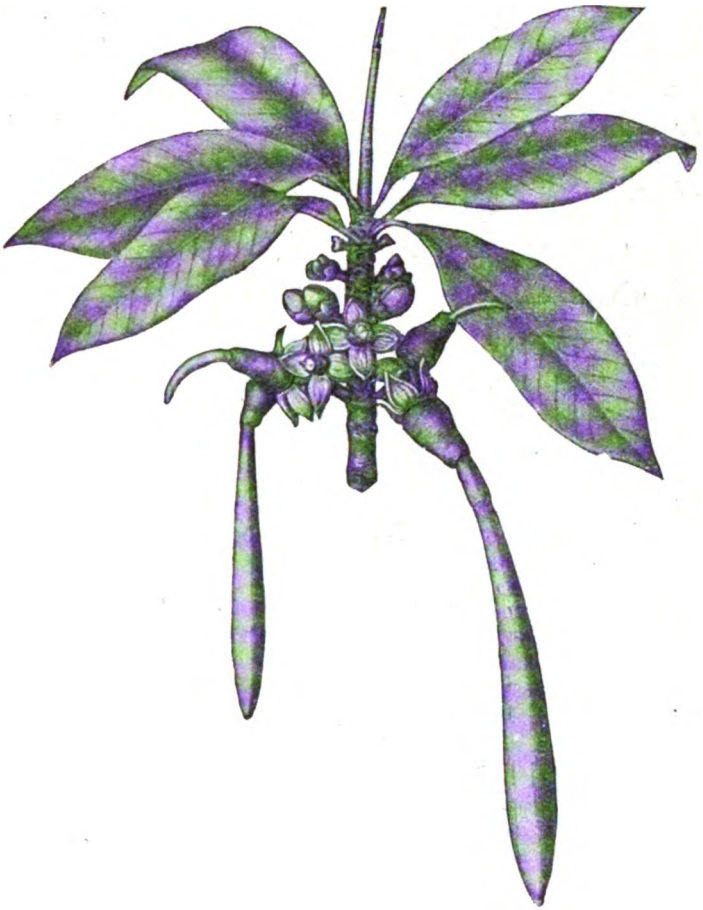


FIG. 716.—*Rhizophora conjugata* (¼ nat. size).

is partly due to the distance apart of the individual trees. *E. amygdalina*, which reaches a height of 150 m. and a circumference of 30 m. at the base of the trunk, is one of the largest forest trees known. *Psidium guayava* and some species of *Eugenia* bear edible fruits; the former is especially valued. *Eugenia caryophyllata* (Moluccas) is of economic importance, its unopened flower-buds forming Cloves (Fig. 718). This tree is commonly cultivated in the tropics. In Fig. 718 the inferior ovary, formed of two carpels, is also seen in longitudinal section.

Species of *Sonneratia* are frequently the constituents of the mangrove vegetation that advance farthest into the sea; their pneumatophores therefore attain a considerable height (Fig. 188).

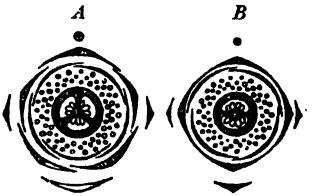


FIG. 717.—Floral diagrams of Myrtaceae. *A*, *Myrtus communis*. *B*, *Eugenia aromatica*. (After EICHLER.)

OFFICIAL. — *Eugenia caryophyllata* yields CARYOPHYLLUM, Cloves. PIMENTA, Allspice, from *Pimenta officinalis*. OLEUM CAJUPUTI from *Melaleuca leucadendron*, a tree of less height but resembling the Eucalyptus trees; it is cultivated in the Moluccas (Buru) for the sake of the oil it yields; its specific name refers to the white colour of the bark. OLEUM EUCALYPTI and EUCALYPTI GUMMI from *Eucalyptus globulus* and other species.

FIG. 718.—*Eugenia caryophyllata* (⅓ nat. size). Flowering branch. A bud cut in half and an opened flower (about nat. size). *OFFICIAL.*

Family 7. **Punicaceae.**—Single genus *Punica*. *Punica granatum* is a tree

originally introduced from the East and now largely cultivated in the Mediterranean

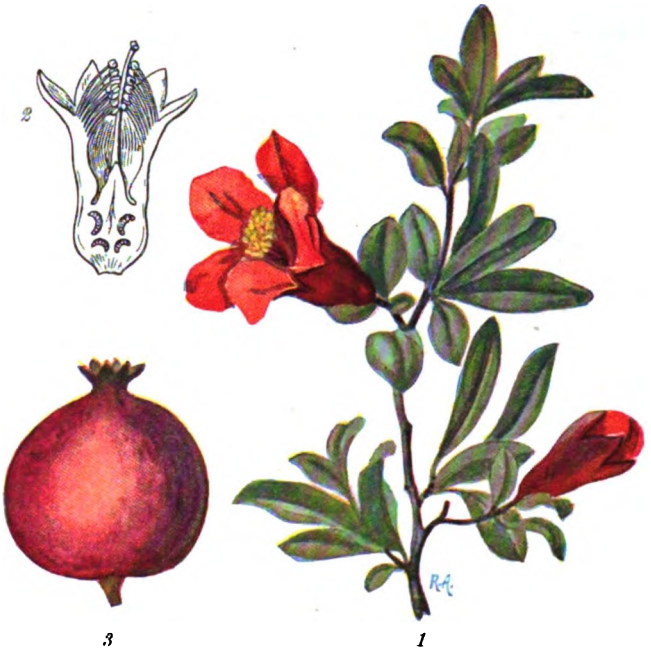


FIG. 719.—*Punica granatum* (½ nat. size). *1*, Branch bearing a flower and a bud. *2*, Flower in longitudinal section. *3*, Fruit. (See text.)

region on account of its acid refreshing fruits known as Pomegranates (Fig. 719). Leaves small, entire. Flower with a stiff, red calyx, an indefinite number of petals, and numerous stamens; the 7-14 carpels are arranged in two tiers, the upper of which corresponds in number to the sepals, the lower to the half of this (Fig. 720). Fruit enclosed by a leathery pericarp with numerous seeds in the loculi of both tiers. The external layers of the seed-coat become succulent and form the edible portion of the fruit.

FIG. 720.—Floral diagram of *Punica granatum*. (After EICHLER.)

Order 21. Umbelliflorae

Inflorescence as a rule an umbel. Flowers hermaphrodite, actinomorphic; a single whorl of stamens and an inferior bilocular ovary, the upper surface of which forms the nectary. Carpels two. A single pendulous ovule in each loculus.

The affinities of the Umbelliflorae are to be sought in the Gruinales to the

Frangulinae. The increasingly tetracyclic floral construction, the formation of a disc in the flower, the formation of secretory reservoirs and canals, and the one-seeded loculi of the fruit are all points of resemblance to the Umbelliflorae.

FIG. 721.—*Cornus mas* (½ nat. size). *1*, Flowering twig. *2*, Twig with fruits. *3*, Flower seen from above. *4*, Flower in longitudinal section. (*3*, *4*, enlarged.)

Family 1. **Cornaceae.**—*Cornus mas*, the Cornelian Cherry (Fig. 721), expands its umbels of tetramerous yellow flowers before the leaves appear. Each umbel is subtended by four bracts. The inflorescences for the succeeding year are already present in the axils of the leaves by the time the fruit is ripe. In Britain two species occur: *C. sanguinea*, the Dogwood, and *C. suecica*, an arctic and alpine plant which reaches its southern limit in Germany.

Family 2. **Araliaceae.**—In Britain the only representative of the family is the Ivy (*Hedera Helix*) ([37]), a root-climber. The elliptical pointed

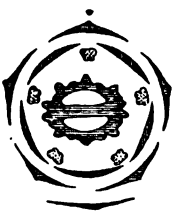


FIG. 722.—Umbelliferae. Floral diagram (*Siler*). (After NOLL.)

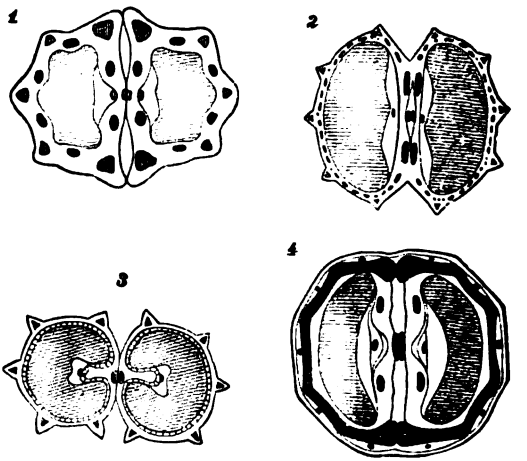


FIG. 723.—Fruits of Umbelliferae in cross section. *1*, *Foeniculum capillaceum*. *2*, *Pimpinella anisum*. *3*, *Conium maculatum*. *4*, *Coriandrum sativum* (*4* modified after a figure by DRUDE).

leaf form appears on the orthotropous shoots of older plants, which in late

summer or autumn bear the flowers. The leaves of the creeping or climbing plagiotropous shoots are lobed and usually have shorter stalks. Calyx with five pointed sepals corresponding to the five ribs on the inferior ovary. The corolla is greenish in tint; the large disc on the upper surface of the ovary attracts the visits of flies and bees. The fruits ripen during the winter and become blackish-blue berries; these are eaten by birds and in this way the seeds are distributed.

FIG. 724.—*Carum carvi* (½ nat. size). Inflorescence bearing fruits. Single flower, and carpophore bearing the mericarps (enlarged). *OFFICIAL.*

Family 3. Umbelliferae.—Herbaceous plants sometimes of large size. The stem, which has hollow internodes and enlarged nodes, bears alternate leaves; these completely encircle the stem with their sheathing base, which is often of large size. The leaves are only rarely simple; usually they are highly compound. Inflorescence terminal, frequently overtopped by the next younger lateral shoot. It is an umbel, or more frequently a compound umbel, the bracts forming the involucre and partial involucres, or an involucre may be wanting. Flowers white, greenish, or yellow; other colours are rare. K 5, C 5, A 5, G $(\bar{2})$. The sepals are usually represented by short teeth. The flowers at the circumference of the compound umbel sometimes become zygomorphic by the enlargement of the outwardly directed petals. Ovary always bicarpellary and bilocular; in each loculus a single ovule which hangs from the median septum with its micropyle directed upwards and outwards. The upper surface of the carpels is occupied by a swollen, nectar-secreting disc continuing into the longer or shorter styles, which terminate in spherical stigmas. Fruit a schizocarp, splitting in the plane of the septum into two partial fruits or mericarps. In many cases the latter remain for a time attached to the carpophore, which originates from the central portion of the septum; this separates from the rest of the septum and bears the mericarps hanging from its upper forked end (Figs. 722-728).

The main areas of distribution of the Umbelliferae are the steppe region of Western Asia, Central North America, Chile, and Australia.

For systematic purposes the fruits are of great importance. Each half of the fruit has five ribs, beneath which the vascular bundles lie. The marginal ribs of each partial fruit frequently lie close together at the septum or they may be distinct; they may resemble the three dorsal ribs or differ more or less from them. Between the five primary ribs four secondary ribs are sometimes present. Usually

FIG. 725.—*Cicuta virosa*. Rhizome cut through longitudinally (½ nat. size). Fruit (enlarged). *Poisonous.*

furrows (valleculae) occur between the ridges, and beneath each furrow a large oil duct (vitta) is found, extending the whole length of the fruit. On either side of the carpophore a similar oil duct is present in the septum, so that each mericarp has six of these vittae (Fig. 723, 1). In some species additional small ducts are present (Fig. 723, 2, 3). The form of the fruit as seen in a cross section differs according to whether the diameter is greater in the plane of the septum or at right angles to this. The character of the marginal and dorsal ridges and the

presence or absence of secondary ridges or vittae serve to distinguish the fruits, and are indispensable aids in determining the species. Since many of the fruits are employed in medicine or as spices, while others are poisonous, their distinction becomes a matter of importance. The endosperm of the seeds contains a fatty oil as reserve material.

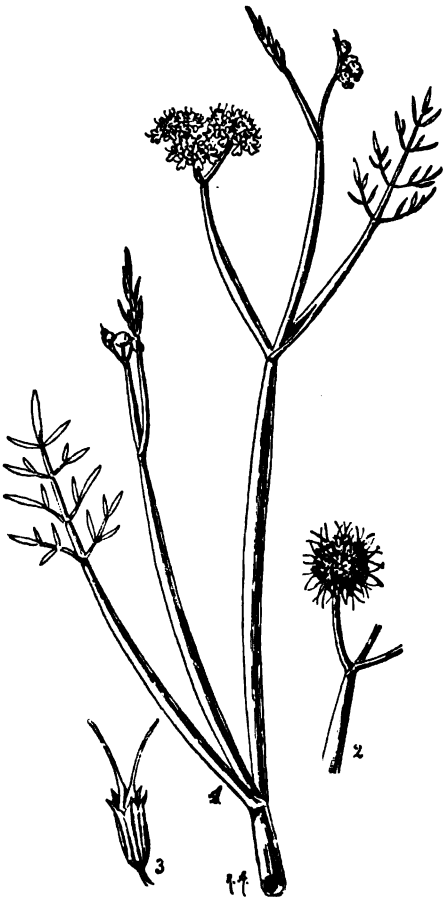


FIG. 726.—*1*, *Oenanthe fistulosa* (½ nat. size). *2*, Group of fruits. *3*, Single fruit (enlarged). *POISONOUS.*

In the following genera the endosperm is flat or slightly convex on the ventral side (Fig. 723, 1, 2). *Pimpinella*, Burnet-Saxifrage. *P. anisum*, Anise, is an annual plant, the seedlings of which exhibit increasing subdivision of the lamina in successive leaves. *Carum carvi*, Carraway, has long been cultivated (Fig. 724); leaves bipinnate, the lowest pinnae resembling stipules. The large lower pinnules are usually placed horizontally on the vertical rachis of the leaf; the terminal pinnules are simple and linear. The terminal umbel, the flowers of

which open first, is overtopped by the lateral umbels arising from the leaf-axils. Biennial. *Foeniculum* (Fennel) and *Levisticum* (Lovage) have yellow flowers. *Petroselinum* (Parsley), *Pastinaca* (Parsnip), *Daucus* (Carrot), *Apium* (Celery), and *Anethum* (Dill), are used as vegetables. *Cicuta* (Water-Hemlock, Fig. 725), *Sium* (Water-Parsnip), *Oenanthe* (Fig. 726) and *Berula*, are marsh- or water-plants. *Aethusa cynapium* (Fool's Parsley, Fig. 727) has the ribs of the fruit keeled; umbels with three elongated, linear, involucral leaves directed outwards. All the last-named plants are poisonous. *Archangelica officinalis* is a conspicuous plant

FIG. 727.—*Aethusa cynapium* (⅓ nat. size). *B*, Single umbel. *C*, Fruit (enlarged). *POISONOUS.*

reaching a height of 2 metres, with large bipinnate leaves provided with saccate, sheathing bases; the greenish flowers are markedly protandrous.

In the following genera the ventral side of the endosperm is traversed by a longitudinal groove. *Scandix*, *Anthriscus* (Beaked Parsley), *Chaerophyllum* (Chervil). *Conium maculatum*, the Hemlock, is a biennial plant often of considerable height; it is completely glabrous, the stem and leaf-stalks often with purple spots; leaves dull green, bi- to tri-pinnate. The ultimate segments end in a small, colourless, bristle-like tip. Fruit with wavy, crenate ridges and without oil-ducts in the valleculae. The whole plant has a peculiar, unpleasant odour (Fig. 728).

The ventral side of the endosperm is concave (Fig. 661, 4). *Coriandrum sativum* is an annual plant; flowers zygomorphic owing to the enlargement of the sepals and petals at the periphery of the umbel. Fruit spherical; mericarps

FIG. 728.—*Conium maculatum* (½ nat. size). *POISONOUS.*

closely united, with ill-marked primary ridges and somewhat more distinct secondary ridges.

OFFICIAL. — *Ferula foetida* (Persia), ASAFETIDA. *Dorema Ammoniacum* (Persia), AMMONIACUM. *Pimpinella anisum*, ANISI FRUCTUS. *Coriandrum sativum*, CORIANDRI FRUCTUS. *Foeniculum capillaceum*, FOENICULI FRUCTUS. *Carum carvi*, CARUI FRUCTUS. *Carum copticum*, *Anethum* (*Peucedanum*) *graveolens*, ANETHI FRUCTUS.

Series II. Sympetalae

The common character of all Sympetalae is afforded by the perianth which consists of a calyx and a gamopetalous corolla. The flowers are, without exception, cyclic. The number of whorls is either five or four, and on this distinction the two groups *Pentacyclicae* and *Tetracyclicae* are based. The Sympetalae does not correspond to a single closely related group but is composed of derivations of a number of natural series which have attained a similar high condition by progressive reduction in the number of members in the individual whorls and in the number of the whorls. Thus the common character of a gamopetalous corolla is purely superficial. Though the distribution of the various groups of Sympetalae in relation to those of the Choripetalae is not adopted here, this is for reasons of space and because the affinities of all the groups are not as yet certain.

From what has been said it follows that the most natural arrangement is according to the height of organisation, *i.e.* to the degree of reduction that has been reached. The Pentacyclicae are therefore placed first and followed by the Tetracyclicae.

A. Pentacyclicae

Order 1. Ericinae

Family 1. **Ericaceae.** — Evergreen, shrubby plants with small, often needle-shaped leaves. Anthers characterised by the possession

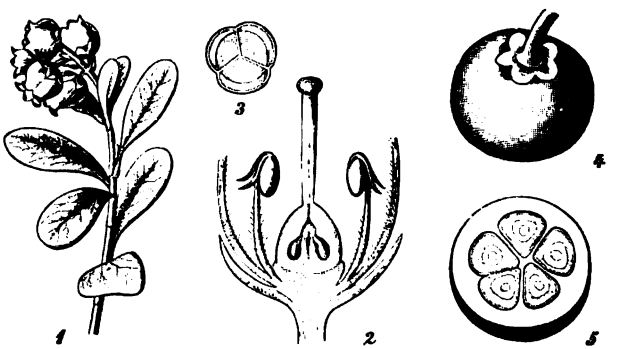


Fig. 729.—*Arctostaphylos Uva ursi.* *1*, Flowering branch. *2*, Flower in longitudinal section. *3*, Pollen tetrad. *4*, Fruit. *5*, Fruit in transverse section. (After Berg and Schmidt.) *Official.*

of an "exothecium" (p. 545), opening by pores or splits, frequently provided with horn-like appendages, on which account the group is also termed Bicornes.

Flowers which are pentamerous in all five whorls are found in the species of *Rhododendron* or Alpine Rose, in *Ledum palustre*, and *Andromeda*; all these have a capsular fruit derived from the superior ovary. *Arctostaphylos Uva ursi* is similar, but the fruit is a drupe (Fig. 729). Pentamerous flowers with an inferior ovary which becomes a berry are found in the genus *Vaccinium* (Fig. 730), *V. vitis idea*, Cowberry, *V. myrtillus*, Blaeberry. The remains of the calyx persist on the summit of the fruit. A reduction of the number of members of the whorls to four is met with in the genus *Erica* with a superior ovary, many species being

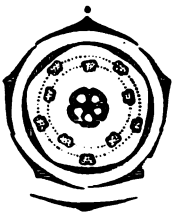


FIG. 730.—Floral diagram of *Vaccinium* (Ericaceae).

FIG. 731.—*Palaquium Gutta*. (½ nat. size. After A. MEYER and SCHUMANN.)

native to the Mediterranean region and the Cape. *Erica tetralix* is distinguished from the closely related Heather, *Calluna vulgaris* (28) by its corolla being longer than the calyx; both are abundant in Britain.

OFFICIAL.—*Arctostaphylos Uva ursi* yields UVAE URSI FOLIA. *Gaultheria procumbens* yields OLEUM GAULTHERIAE.

Order 2. Diospyrinae

The **Sapotaceae** is a tropical family; the plants contain latex. Species of *Palaquium* (Fig. 731) and *Payena* from the Malayan Archipelago are the trees from which gutta-percha is obtained. Balata is obtained from *Mimusops*; trees found throughout the tropics.

Ebenaceae.—*Diospyros Kaki* is a Japanese fruit tree; *D. Ebenum*, ebony.

Styracaceae.—The origin of Benzoin (BENZOINUM), an official resin, from *Styrax Benzoin*, though generally assumed, is open to doubt.

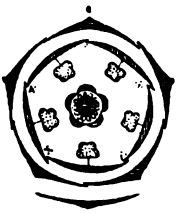


FIG. 732.—Primulaceae. Floral diagram (*Primula*).

FIG. 733.—*Anagallis arvensis* (½ nat. size). Longitudinal section of flower, and capsule at dehiscence (enlarged).

FIG. 734.—*Cyclamen europaeum*. *A*, Entire plant. *B*, Fruit. (After REICHENBACH.) *Poisonous.*

Order 3. Primulinae

Family 1. **Primulaceae.**—The floral diagram (Fig. 732) shows only one whorl of stamens, since these stand opposite the petals; the outer whorl of stamens is absent; in normal Tetracyclicae it is the inner whorl that is missing. The free-central placentation is characteristic. The genus *Primula* is widely distributed; the British species show the superior unilocular ovary with a single style, characteristic of the family; heterostylic. *Anagallis* (Fig. 733), capsule opens by a lid. *Cyclamen* (Fig. 734). The uncooked tubers of *Cyclamen* and *Anagallis*, and the glandular hairs of a number of species of *Primula* (*P. obconica*, *Corthusa matthioli* (29)) are poisonous.

B. TETRACYCLICAE

1. *Ovary Superior*

The *Tetracyclicae* have only four regularly alternating whorls in the flower. They can be divided into two groups of orders according to the position of the ovary. This is superior in the orders Contortae, Tubiflorae, and Personatae; in all these the ovary is composed of two carpels. The orders with an inferior ovary are the Rubiinae and Synandrae. In the Rubiinae the carpels are as a rule two, but sometimes three or one; in the Synandrae which are characterised by the united anthers, the carpels vary from five to three, two, or only one.

These common characters having been recognised, the families within the various orders may be dealt with.

Order 4. Contortae

Plants with decussate, usually simple leaves and actinomorphic flowers, the corolla of which is often contorted in the bud. Stamens epipetalous.

Family 1. **Oleaceae.**—This is readily recognised by the two stamens. The corolla is usually tetramerous as is shown in the floral diagram of *Syringa* (Fig. 735). Besides *Ligustrum*, *Jasminum*, and *Syringa*, *Olea europaea*, the Olive Tree or Olive, is the most important plant of the family (Fig. 736). It is a native of the Mediterranean region, where it is also cultivated. The flower and fruit correspond to the type for the family (Fig. 737). The drupe contains a fatty oil both in the succulent exocarp and in the endosperm (Fig. 738). *Fraxinus*, the Ash, differs from the type of the order in having pinnate leaves; *F. excelsior* has apetalous, anemophilous flowers, which appear before the leaves. *F. ornus*, the Flowering Ash, has a double perianth and is entomophilous; it is polygamous, having hermaphrodite flowers as well as female flowers with black sterile anthers; the corolla is divided to the base. It is cultivated in Sicily for the sake of the mannite it yields.

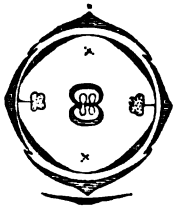


FIG. 735.—Oleaceae. Floral diagram (*Syringa*).

OFFICIAL.—*Olea europaea* yields OLEUM OLIVAE.

Family 2. **Loganiaceae.**—Species of *Strychnos*, which are trees or lianes climbing by means of hook-tendrils, yield the well-known curare of South America, and the arrow poison used by the Malays.

OFFICIAL.—*Strychnos nux vomica* is a small tree or shrub of Southern Asia, the fruits of which are berries with a firm rind; in the succulent pulp a small number of erect, circular, disc-shaped seeds are embedded (Fig. 740). It yields NUX VOMICA and STRYCHNINA. GELSEMII RADIX is obtained from *Gelsemium nitidum*, which is a native of North America.

Family 3. **Gentianaceae.**—This is recognisable by the unilocular ovary and the clearly contorted corolla when in bud (Fig. 741). *Gentiana* is a genus with numerous species. Plants of larger or smaller size, especially abundant in the Alps. Flowers brightly coloured. This genus affords one of the best examples of seasonal dimorphism, *i.e.* the splitting of a species into two closely related forms which develop at different seasons. Since the

FIG. 736.—*Olea europaea* in fruit (½ nat. size). OFFICIAL.

FIG. 737.—*Olea europaea*. *A*, Corolla spread out. *B*, Calyx and ovary in longitudinal section. (Enlarged. After ENGLER-PRANTL.)

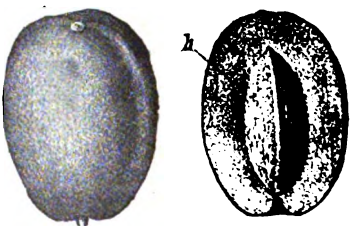


FIG. 738.—*Olea europaea*. Drupe. *h*, Stone.

height of the vegetative period of the alpine meadows coincides with their annual mowing, this expresses itself in the distinction of an early form, fruiting before the meadows are cut, and a late form developing after this has taken

place (30). *Erythraea*, Centaury. *Menyanthes*, Bog-Bean. *Limnanthemum*, aquatic plants with floating leaves.

OFFICIAL.—*Gentiana lutea* and other species yield GENTIANAE RADIX. CHIRATA is obtained from *Swertia chirata* (N. India).

Family 4. **Apocynaceae.**—Evergreen plants with latex. Especially numerous in the tropics. Stigma ring-shaped. Carpels only united in the region of the style, free below and separating after fertilisation. Usually two follicles with numerous seeds provided with a tuft of hairs (Figs. 744, 745).

The only British species is *Vinca minor*, the evergreen Periwinkle, occurring

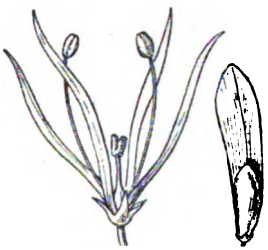


FIG. 739.—*Fraxinus ornus*. Flower and fruit.

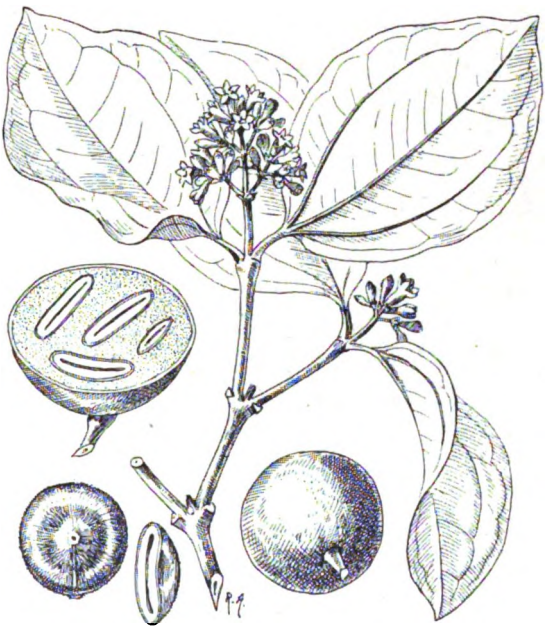


FIG. 740.—*Strychnos nux vomica* (½ nat. size). Fruit and seed whole and in cross-section. OFFICIAL and POISONOUS.

in woods (Fig. 742). *Nerium oleander* (Fig. 743), a native of the Mediterranean region. The floating fruit of *Cerbera Odollam*, from the mangrove vegetation, is shown in Fig. 576.

OFFICIAL.—*Strophanthus kombe* and *S. hispidus* (31) (Fig. 745), lianes of tropical Africa, yield STROPHANTHI SEMINA. A bark is obtained from *Alstonia constricta* and *A. scholaris*.

Caoutchouc (32) is obtained from *Kickxia elastica* and other species, trees of tropical W. Africa. It is also obtained from numerous species of *Landolphia* (*L. Kirkii*, *Heudelotii*, *comorensis*, etc.), *Carpodinus* from tropical Africa. *Hancornia speciosa*, a tree of the dry Brazilian Campos, and *Willoughbeia firma*, *W. flavescens*, and other species of this Malayan genus of lianes, are also rubber-yielding plants. Guttapercha is present in the latex of *Tabernaemontana Donnell Smithii*, Central America.

Family 5. **Asclepiadaceae.**—Similar and closely related to the Apocynaceae but differing in the carpels being free, only united by the prismatic stigma. Stamens united at the base, with dorsal, nectar-secreting appendages forming a corona. The pollen of each pollen sac

is united into a pollinium, the stalk of which is attached to a glandular swelling (adhesive disc) of the angular stigma. These adhesive discs alternate with the stamens so that the two pollinia attached to each disc belong to the halves of two adjoining stamens. Visiting insects remove, as in the Orchidaceae, the pollinia and carry them to another flower (Fig. 746).

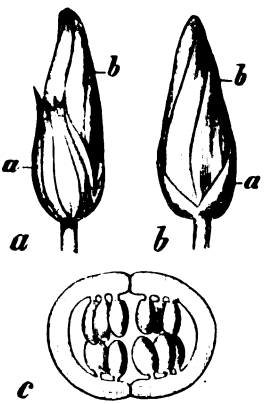


FIG. 741.—*Gentiana lutea*. *a* and *b*, Flower-buds (nat. size), showing calyx (*a*) and twisted corolla (*b*); *c*, transverse section of ovary. OFFICIAL. (After BERG and SCHMIDT.)

FIG. 742.—*Vinca minor* (⅓ nat. size).

Vincetoxicum officinale (Fig. 747) is a European herb with inconspicuous white flowers and hairy seeds which are borne in follicles; poisonous. Other forms are mostly tropical or sub-tropical. The succulent species of *Stapelia*, *Hoodia*, *Trichocaulon*, etc., which resemble Cactaceae in habit, and inhabit S. African deserts, and *Dischidia rafflesiana* (33), the peculiar pitcher plant of the Malayan region, the pitchers of which serve to condense water, deserve special mention. *Hoya carnosa* is frequently cultivated.

OFFICIAL.—*Hemidesmus indicus* yields HEMIDESMI RADIX.

Order 5. Tubiflorae

Flowers pentamerous, actinomorphic, or zygomorphic. Carpels 2. Ovary superior, bilocular, with two ovules, which are frequently

separated by a false septum, in each loculus. The normal number of stamens is reduced in the zygomorphic flowers to four or two. This order may be connected with the Gruinales and Rosiflorae.

FIG. 743.—*Nerium oleander* (⅓ nat. size). *POISONOUS.*

Family 1. **Convolvulaceae.**—Many of the plants of this family are twining plants with alternate sagittate leaves and wide, actinomorphic, funnel-shaped corolla, which is longitudinally folded in the bud. Ovules erect; fruit a capsule.

Convolvulus arvensis, a perennial, twining, herbaceous plant occurring everywhere by waysides, and as a weed in corn-fields. Flowers solitary, long-stalked,

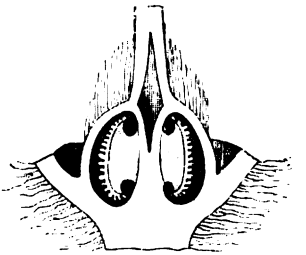


FIG. 744.—*Strophanthus hispidus.* Ovary in longitudinal section. (4/1; after ENGLER-PRANTL.)

FIG. 745.—*Strophanthus hispidus* (1/4 nat. size. After MEYER and SCHUMANN). Fruit (1/4 nat. size). Seed (1/3 nat. size). (After SCHUMANN in ENGLER-PRANTL.) *OFFICIAL.*

situated in the axils of the leaves and sometimes in the axils of the bracteoles of another flower. *Calystegia* has two large bracteoles placed immediately beneath the calyx. *C. sepium.* The Dodder (*Cuscuta*) is a slender parasitic plant containing very little chlorophyll, which attaches itself by means of haustoria to a

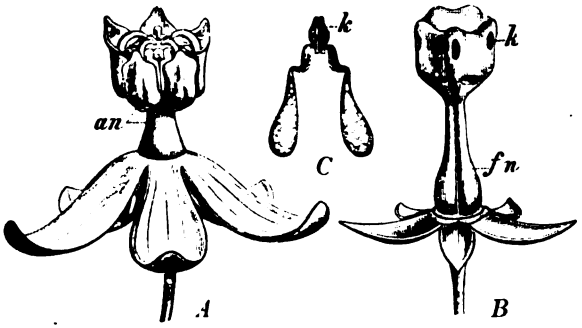


FIG. 746.—*Asclepias curassavica*. *A*, Flower; *an*, androecium (× 4). *B*, Calyx and gynaeceum; *fn*, ovary; *k*, adhesive discs (× 6). *C*, Pollinia (more highly magnified). (After BAILLON.)

FIG. 747.—*Vincetoxicum officinale* (½ nat. size). *POISONOUS.*

FIG. 748.—*Exogonium purga* (½ nat. size. After BERG and SCHMIDT). *OFFICIAL.*

number of different host plants (Fig. 221). *Ipomaea*: several species are cultivated as ornamental plants. *I. pescaprae* is one of the strand plants of tropical countries.

OFFICIAL.—JALAPA is obtained from *Exogonium purga* (Fig. 748), a twining plant, with tuberous lateral roots, occurring on the wooded eastern slopes of the Mexican tableland. *Ipomaea hederacea, I. orizabensis, I. turpethum.* SCAMMONIAE RADIX is the dried root of *Convolvulus Scammonia* (Asia Minor).

Family 2. **Boraginaceae.**—Contains herbs usually covered with coarse hairs. *Symphytum* (Comfrey), *Borago* (Borage), *Anchusa* (Alkanet), *Echium* (Bugloss) (Fig. 750), *Myosotis* (Forget-me-not), are among the commonest and most conspicuous herbaceous plants of our flora; all have entire, alternate leaves, covered with harsh hairs and relatively large flowers of a lighter or darker blue, grouped in complicated inflorescences. Flowers actinomorphic or zygomorphic. Petals frequently provided with scales standing in the throat of the corolla. Ovary always bilocular but divided by false septa into four one-seeded nutlets. The style springs from the midst of the four-lobed ovary.

FIG. 749.—*Borago officinalis*. *a*, Flower; *b* and *c*, fruit (nat. size).

FIG. 750.—*Echium vulgare*. Inflorescence (½ nat. size). Single flower and fruit, composed of four nutlets (enlarged).

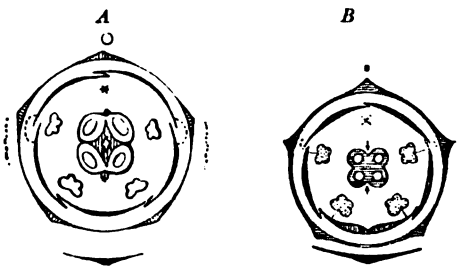


FIG. 751.—Floral diagrams of (*A*) *Verbena officinalis* (after EICHLER), and (*B*) *Lamium* (Labiatae) (after NOLL).

Family 3. **Verbenaceae.**—Clearly dorsiventral flowers, with only four stamens; the ovary contains only four ovules (Fig. 751), but the style is terminal. *Tectona grandis*, Teak-tree; *Avicennia* (33) a viviparous mangrove plant.

Family 4. **Labiatae.**—Distributed over the earth. Herbs or shrubs with quadrangular stems and decussate leaves without stipules. Leaves simple; plants often aromatic owing to the presence of glandular

hairs. Flowers solitary in the axils of the leaves, or forming apparent whorls. The small inflorescences are dichasia or double cincinni, and are often united in larger spike- or capitulum-like inflorescences. Flower zygomorphic (Fig. 751). Calyx gamosepalous, with five teeth; corolla two-lipped, the upper lip consisting of two, the lower of three petals; stamens in two pairs, two long and two short, rarely only two (*Salvia*, *Rosmarinus*). The ovary (Fig. 751) corresponds to that of the Boraginaceae; it has a ring-shaped nectary at the base.

The Labiatae include a considerable proportion of our commonest native spring and summer flowers; *Lamium*, *Galeopsis* (Fig. 752), and *Stachys* have the upper lip helmet-shaped, *Ajuga* has it very short, while in *Teucrium* the

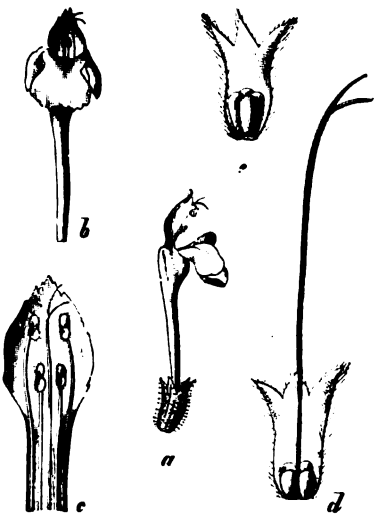


FIG. 752.—*Galeopsis ochroleuca*. *a*, Flower; *b*, the same with calyx removed; *c*, corolla cut open, showing stamens and style; *d*, calyx and gynaeceum; *e*, fruit. (*a*, *b*, nat. size; *c*, *d*, *e* × 2.)

FIG. 753.—*Lavandula vera* (½ nat. size). OFFICIAL.

upper lip is deeply divided.

Fig. 754.—*Salvia officinalis*. Flowering shoot (½ nat. size). Tubular corolla slit open to display the stamens (enlarged).

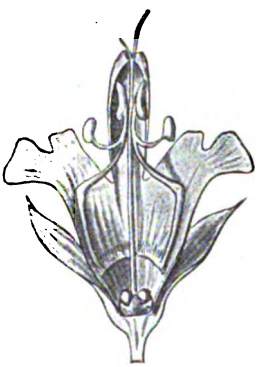
Nepeta and *Glechoma* differ from the majority of the order, in having the posterior stamens longer than those of the anterior pair. *Salvia*, Sage, has the two stamens that remain peculiarly constructed in relation to pollination (Fig. 754, cf. Fig. 528). Many Labiatae are of value on account of their aromatic properties. They are especially abundant in the xerophytic formation of shrubby plants in the Mediterranean region to which the name Maquis is given.

OFFICIAL.—*Rosmarinus officinalis* yields OLEUM ROSMARINI. *Lavandula vera* (Fig. 753) (Mediterranean region), OLEUM LAVANDULAE. *Mentha piperita*, OLEUM MENTHAE PIPERITAE. *M. viridis*, OLEUM MENTHAE VIRIDIS. *M. arvensis* and *M. piperita* yield MENTHOL. *Thymus vulgaris* and *Monarda punctata* yield THYMOL.

Order 6. Personatae

The Personatae are of common origin with the Tubiflorae. The flowers are actinomorphic or zygomorphic. There are, however, no false septa in the ovary, and the number of ovules is usually a larger one.

Family 1. **Solanaceae**.—Herbs or small woody plants, with nearly always actinomorphic flowers. Petals plaited. Ovary bilocular, septum inclined obliquely to the median plane. Ovules numerous, on a thick placenta (Fig. 755). Fruit, a capsule or a berry. Seeds with endosperm; embryo usually curved. Anatomically the order is characterised by possessing bicollateral vascular bundles.



Many species of *Solanum* occur as weeds. Flowers actinomorphic; fruit a berry. *S. nigrum*, Nightshade. *S. dulcamara*, Bitter-sweet (Fig. 756), is a shrubby plant, climbing by means of its stems and petioles, and especially common in thickets by the banks of

streams and similar situations. *S. tuberosum*, the potato. *Lycopersicum*, the tomato. On graft-hybrids, periclinal chimaeras and gigas-forms of *Solanum*, cf. p. 299 and H. WINCKLER (34). The Deadly Night-shade, *Atropa belladonna* (Fig. 757), a very poisonous shrubby plant occurring in Europe, is recognisable by the actinomorphic flowers, with a short, wide, tubular corolla of a dirty purple colour. The main shoot is, to begin with, radial, but branches below the terminal flower into, as a rule, three equally vigorous lateral shoots, which exhibit further cicinnal branching. By the carrying up of the subtending bract upon the lateral shoot an appearance of paired leaves is brought about. *Capsicum annuum*, Spanish Pepper, has a dry, berry-like fruit. It resembles *Atropa* in its branching and the position of its leaves. *Datura Stramonium*, Thorn-apple (Fig. 758), is an annual plant, widely spread in Europe, Asia, and N. America. It has

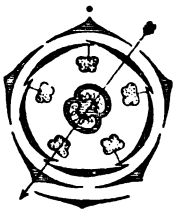


FIG. 755.—Solanaceae. Floral diagram (*Petunia*). (After NOLL.)

FIG. 756.—*Solanum dulcamara* (½ nat. size). *POISONOUS.*

incised, palmately-veined leaves, large, white, terminal flowers, and spiny fruits. *Nicotiana tabacum* (Fig. 759) is a South American plant with numerous cultivated varieties. Its large alternate leaves, which bear numerous glandular hairs, form TOBACCO, after being dried and prepared. *Hyoscyamus niger*, the

Henbane (Fig. 760), is an annual plant occurring in Central Europe, North Africa, and Western Asia. The leaves are clothed with glandular hairs. Flowers slightly

FIG. 757.—*Atropa belladonna* (½ nat. size). *OFFICIAL* and *POISONOUS*.

zygomorphic, of dull yellowish-violet colour with darker markings; inflorescence, a cincinnus. Fruit a pyxidium.

All Solanaceae are more or less poisonous partly on account of the presence of

considerable amounts of alkaloids or poisonous glucosides. Species of *Solanum*,

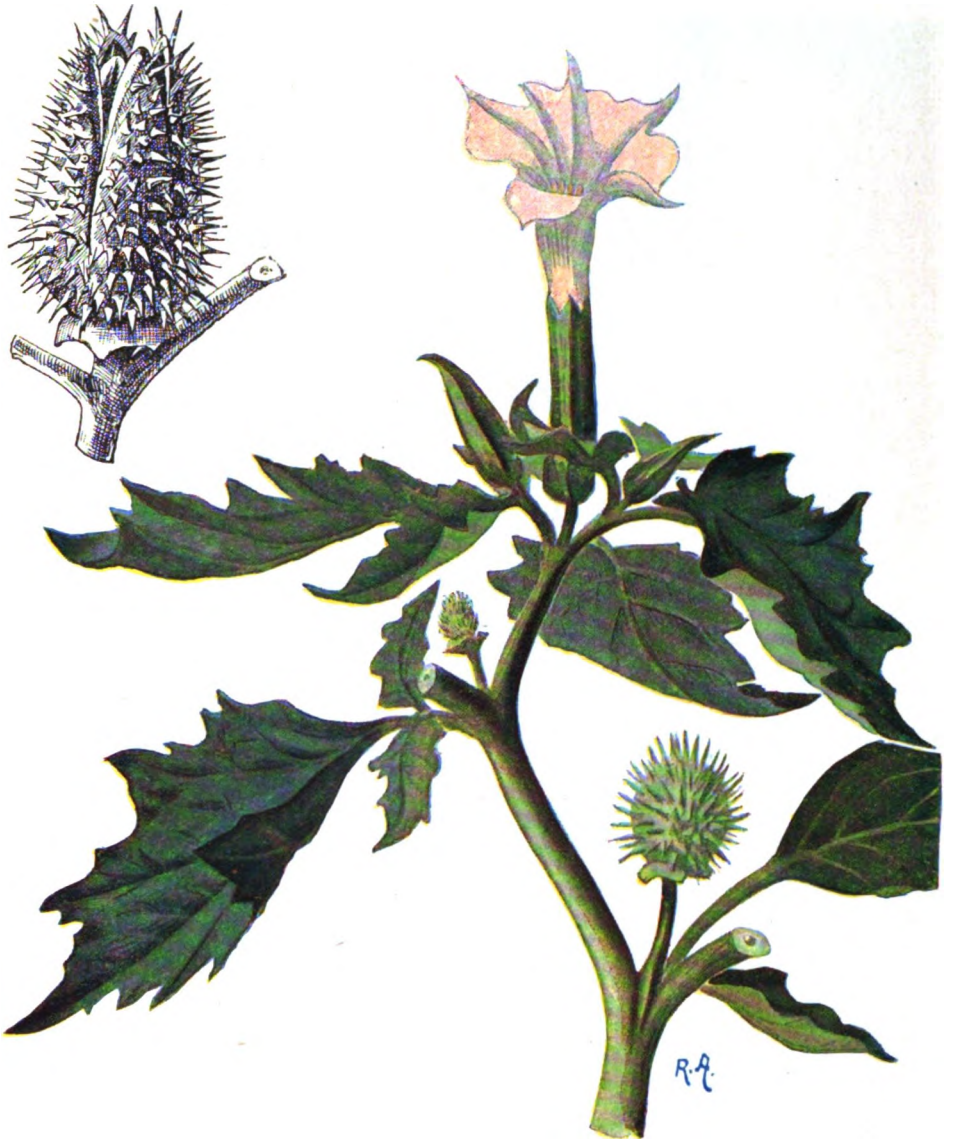


FIG. 758.—*Datura Stramonium* (½ nat. size). Mature fruit after dehiscence.
OFFICIAL and *POISONOUS*.

Atropa, *Datura*, *Hyoscyamus*, and *Nicotiana* are among the most poisonous plants met with in this country.

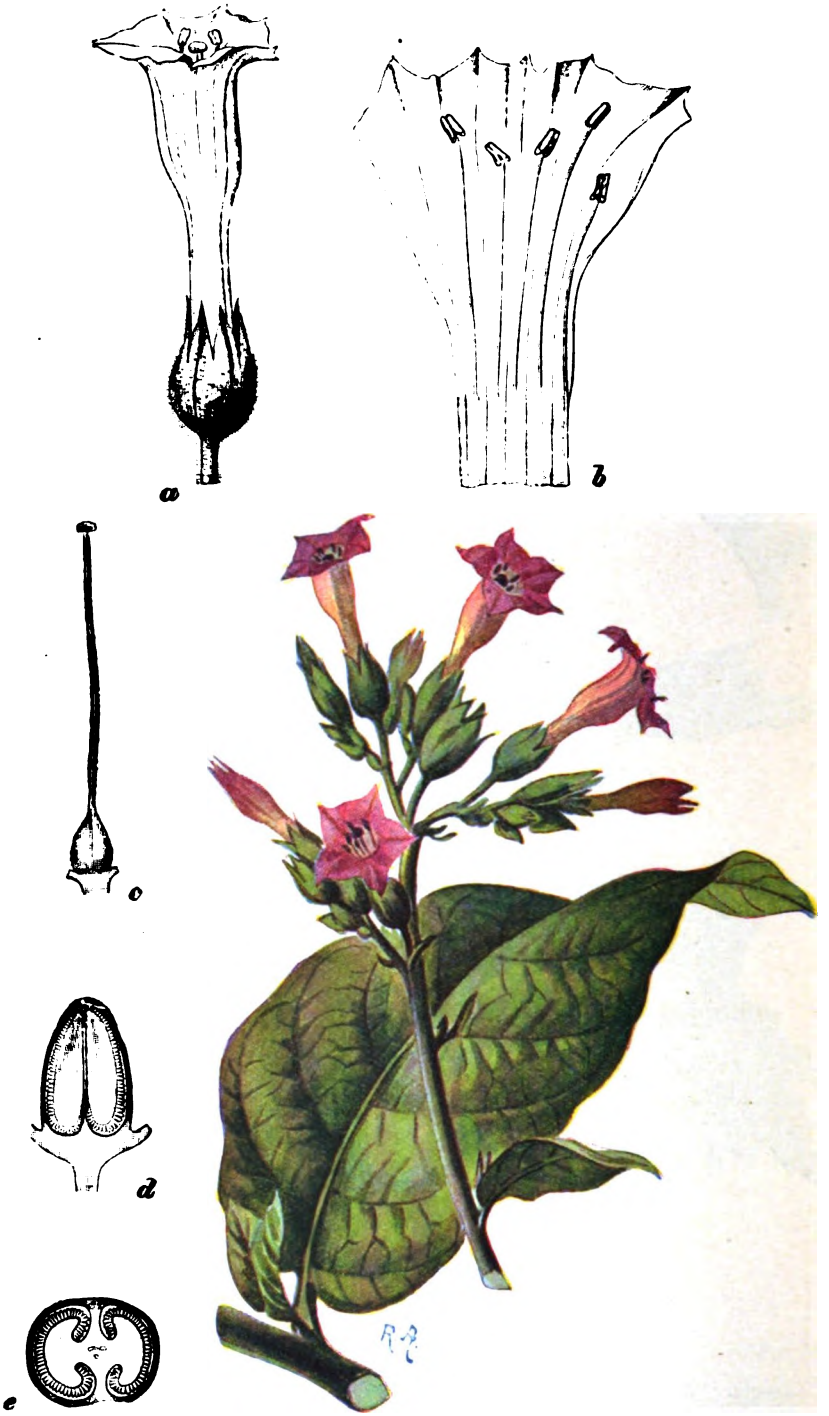


FIG. 759.—*Nicotiana tabacum* (½ nat. size). *Poisonous.* *a*, Flower; *b*, corolla cut open and spread out flat; *c*, ovary; *d* and *e*, young fruit. (*a*, *b*, *c*, nat. size; *d*, *e* × 2.)

FIG. 760.—*Hyoscyamus niger.* Flowering shoot and fruit (½ nat. size). *OFFICIAL* and *POISONOUS.*

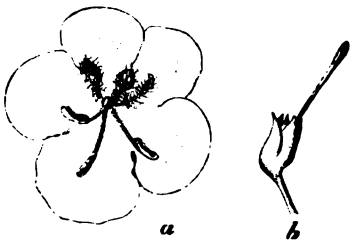


FIG. 761.—*Verbascum thapsiforme.* *a*, Flower; *b*, calyx and style (nat. size).

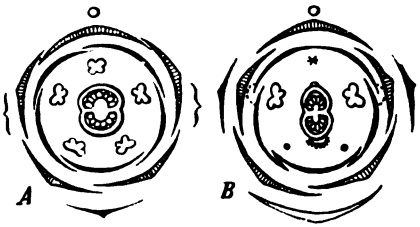


FIG. 762.—Scrophulariaceae. Floral diagrams. *A*, *Verbascum*. *B*, *Gratiola*. (After EICHLER.)

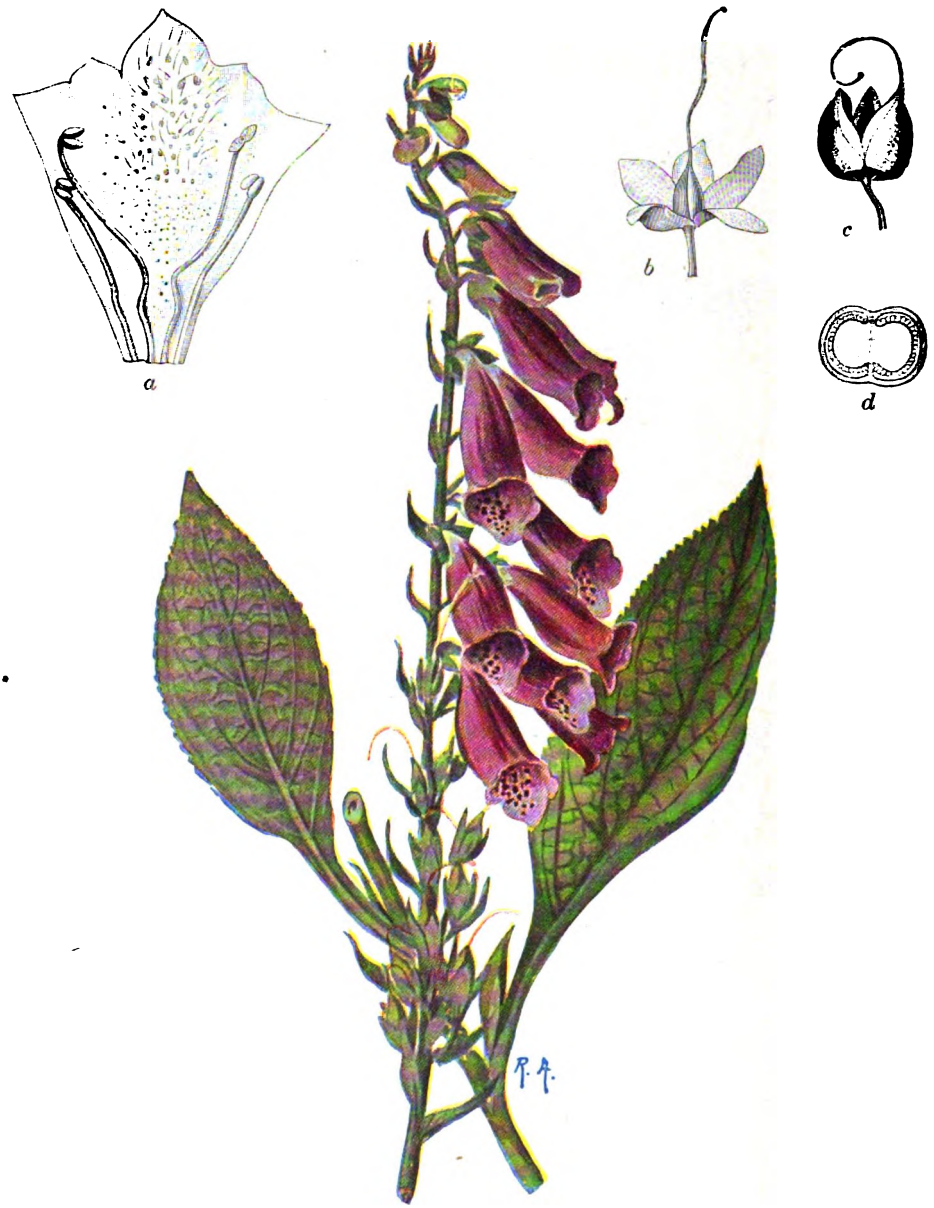


FIG. 763.—*Digitalis purpurea* (½ nat. size). *a*, Corolla cut open and spread out; *b*, calyx and pistil; *c*, fruit after dehiscence; *d*, transverse section of fruit (nat. size). *OFFICIAL* and *POISONOUS*.

OFFICIAL. — *Capsicum minimum* yields CAPSICI FRUCTUS. *Atropa belladonna* yields BELLADONNAE FOLIA, BELLADONNAE RADIX, and ATROPINA. *Datura Stramonium*, STRAMONII SEMINA and STRAMONII FOLIA. *D. fastuosa*, *D. metel*. *Hyoscyamus niger*, HYOSCYAMI FOLIA.

Family 2. Scrophulariaceae. — Flowers zygomorphic. Corolla not plaited in the bud. Number of stamens nearly always incomplete. Carpels median. Fruit, a bilocular capsule.

Verbascum (Fig. 761), the Mullein; biennial herbs, which in the first season form a large rosette of woolly leaves from which the erect inflorescence arises in the second year. The single flowers have five stamens, and are only slightly zygomorphic; the three posterior stamens have hairy filaments, and are further distinguished from the two anterior stamens by the transverse position of their anthers. *Linaria* and *Antirrhinum* have a two-lipped corolla with four stamens. *Digitalis*, Foxglove (Fig. 763), has an obliquely campanulate corolla and four stamens. The flowers hang from one side of the ascending raceme, which is produced in the second year. *Gratiola* and *Veronica* with only two fertile stamens.

FIG. 764.—*Orobanche minor*, parasitic on *Trifolium repens* (½ nat. size). Single flower (enlarged).

A special group includes a number of closely related genera which have adopted a more or less completely parasitic mode of life. The most completely parasitic form is *Lathraea* (35), the species of which have no trace of chlorophyll; *L. squamaria*, the Toothwort, is parasitic on the roots of the Hazel. Many (*e.g. Tozzia, Bartsia, Euphrasia, Odontites, Pedicularis, Melampyrum, Alectorolophus*) are semiparasitic. Although they possess green leaves they attach themselves by means of haustoria to the roots of other plants, from which they obtain nutrient materials.

OFFICIAL.—*Digitalis purpurea* yields DIGITALIS FOLIA. *Picorhiza kurroa.*

Family 3. **Orobanchaceae.**—Root-parasites, without chlorophyll. Flower as in the Scrophulariaceae, but with a unilocular ovary. Several British species of *Orobanche*, parasitic on various host plants (Fig. 764).

Family 4. **Lentibulariaceae.**—Marsh- or water-plants. They capture and digest insects. *Utricularia* (36), *Pinguicula.*

Family 5. **Plantaginaceae.**—Reduced forms. *Litorella lacustris. Plantago.* Plantain; anemophilous, and protogynous.

OFFICIAL.—*Plantago ovata.*

2. *Ovary Inferior*

Order 7. Rubiinae

This order is related to the Umbelliflorae, where also the ovary is inferior. The flowers are tetramerous or pentamerous; the numbers of stamens and carpels vary in the zygomorphic and asymmetric flowers.

Family 1. **Rubiaceae** (37).—Herbs, shrubs, or trees, with simple decussate leaves and stipules. Flowers actinomorphic. Ovary bilocular.

The few native Rubiaceae all belong to the group represented by *Asperula* (Woodruff), *Galium, Rubia.* These genera are characterised by the resemblance of the stipules to the leaves; usually a whorl of six members is borne at each node, but sometimes it is reduced to four by the union of the stipules in pairs; the numbers may, however, vary.

In the tropics the Rubiaceae are abundantly represented by trees, shrubs, climbers, and epiphytes. One of the most important Rubiaceae is *Cinchona*, a genus from the S. American Andes, now cultivated in the mountains of nearly all tropical colonies (Fig. 765). Stipules deciduous. Flowers in terminal panicles; corolla tubular, with an expanded terminal portion fringed at the margin. Fruit, a capsule, with winged seeds (Fig. 766). *Coffea*, the Coffee plant, is a shrub; *C. arabica* (Fig. 767) and *C. liberica* are important economic plants, originally derived from Africa, and now cultivated throughout the tropics. The fruits are two-seeded drupes. The pericarp becomes differentiated into a succulent exocarp and a thin stony endocarp, which encloses the two seeds with their thin silvery seed-coats. These are the coffee-beans. The noteworthy tuberous epiphytic plants *Hydnophytum* and *Myrmecodia* (37) have also succulent fruits; according to the most recent investigations they utilise the excreta of the ants which inhabit the cavities in the stems. Species of *Psychotria* and *Pavetta* are also of physio-

logical interest on account of the nitrogen-fixing bacteria harboured in their leaves. The association is higher than that of the Leguminosae with the bacteria in their root-nodules in that the bacteria here are present in the seeds and are thus handed on to a new generation.

OFFICIAL.—*Cinchona succirubra* yields CINCHONAE RUBRAE CORTEX. QUININE

FIG. 765.—*Cinchona succirubra* (nat. size). *OFFICIAL.* (After SCHUMANN and ARTHUR MEYER.)

is obtained from this and other species of *Cinchona*. *Uragoga* (*Psychotria*) *Ipecacuanha* yields IPECACUANHA. CATECHU is obtained from *Ourouparia* (*Uncaria*) *gambir*.

Family 2. **Caprifoliaceae.**—Woody plants, usually without stipules. *Viburnum* has actinomorphic flowers with a trilocular ovary. The fruit contains only one seed. The sterile marginal flowers, which are alone represented in cultivated forms,

serve as the attractive apparatus. *Sambucus*, Elder, has imparipinnate leaves, glandular stipules, and actinomorphic flowers. Zygomorphic flowers are found in the Honeysuckle (*Lonicera periclymenum*), one of our native lianes; the long-tubed, sweet-scented flowers are attractive to long-tongued Sphingidae. *Diervilla* (*Weigelia*) a favourite ornamental shrub.

OFFICIAL.—*Viburnum prunifolium*.

Family 3. **Valerianaceae.**—Herbs or small shrubs, with decussately-arranged leaves and asymmetrical flowers. Calyx only developed on the fruit as a "pappus,"

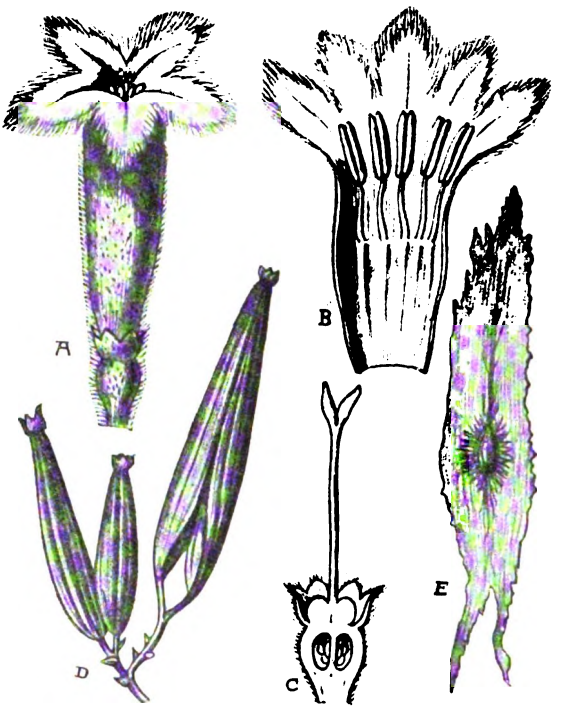


FIG. 766.—*Cinchona succirubra*. *A*, Flower. *B*, Corolla split open. *C*, Ovary in longitudinal section. *D*, Fruit. *E*, Seed. (*D* nat. size, the others enlarged.) (After A. MEYER and SCHUMANN.) *OFFICIAL.*

i.e. a feathery crown assisting in wind-dispersal. *Valeriana*, the Valerian (Figs. 769, 770), has a spurred pentamerous corolla, three stamens, and three carpels, only one of which is fertile.

OFFICIAL.—*Valeriana officinalis* yields VALERIANAE RHIZOMA. *V. Wallichii*.

Family 4. **Dipsaceae.**—Herbaceous plants with opposite leaves and tetramerous or pentamerous actinomorphic or zygomorphic flowers. The individual flowers have an epicalyx which persists on the fruit and serves as a means of dispersal; they are associated in heads surrounded by sterile bracts.

Dipsacus, the Teazel, has recurved hooks on the involucral and floral bracts. Corolla with four lobes, four stamens, and one carpel containing a pendulous, ana-

tropous ovule; endosperm present in the seed (Fig. 771). *Succisa* (Fig. 772) has a four-lobed corolla; bracts are present on the common receptacle. *Scabiosa*

FIG. 767.—*Coffea arabica* (½ nat. size). Single flower, fruit, seed enclosed in endocarp, and freed from it (about nat. size).

has the marginal flowers of the head larger and dorsiventral. *Knautia* has tetramerous flowers; no floral bracts.

Order 8. Synandrae

The common character of this eighth and last order is found in the fact that the stamens in one way or another are fused or united together. The flowers may be actinomorphic or zygomorphic.

Family 1. **Cucurbitaceae.**—This family, in the frequently incomplete sympetaly it exhibits, shows a relationship to the Choripetalae, although to groups which have not been mentioned in this short survey. The Cucurbitaceae include herbaceous, coarsely hairy, large-leaved plants. Flowers diclinous; monoecious or less commonly dioecious. Calyx and corolla adherent below. Anthers united in pairs or all coherent; ∞-shaped. Ovary trilocular (Fig. 773). Fruit, a berry,

FIG. 768.—*Uragoga Ipecacuanha* (½ nat. size). Infrutescence by the side. *OFFICIAL.*

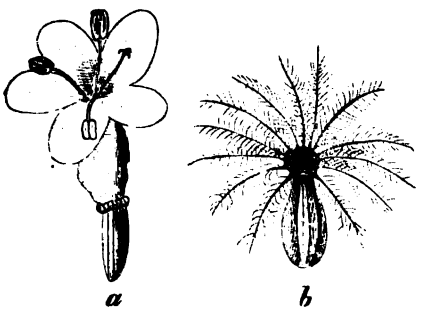


FIG. 769.—*Valeriana officinalis.* *a*, Flower (× 8); *b*, fruit (enlarged). *OFFICIAL.*

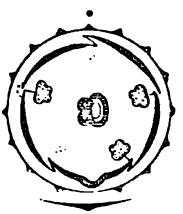


FIG. 770.—*Valeriana.* Floral diagram. (After NOLL.)

with a firm rind. The branched or unbranched tendrils correspond in their lateral position to a bract. *Cucumis sativus*, the Cucumber, and *Cucumis Melo*, the Melon, are commonly cultivated. The Cucumber is parthenocarpic ([38]), *i.e.* pollination of the stigma is not necessary for the setting of the fruit. *Cucurbita Pepo*, the Pumpkin. *Bryonia*, Bryony. *Citrullus Colocynthis* is a perennial plant inhabiting

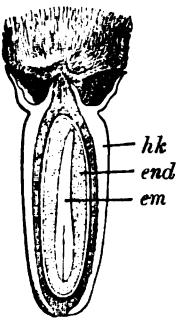


FIG. 771. — Fruit of *Dipsacus fullonum* in longitudinal section. *hk*, Calyx tube; *end*, endosperm; *em*, embryo. (After BAILLON.)

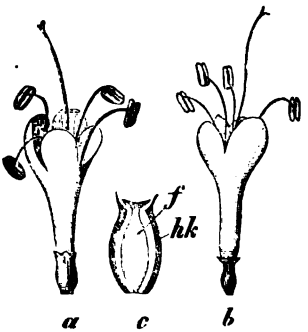


FIG. 772.—*Succisa pratensis*. *a*, Flower with epicalyx; *b*, the same after removal of epicalyx; *c*, fruit in longitudinal section; *f*, ovary; *hk*, epicalyx. (After H. SCHENCK.)

the Asiatic and African deserts north of the equator. Leaves deeply three-lobed and pinnately divided. Tendrils simple or forked; male and female flowers solitary in the axils of the leaves. The fruit is a dry berry (Fig. 774). *Ecballium elaterium.*

OFFICIAL.—*Citrullus colocynthis* yields COLOCYNTHIDIS PULPA. *Cucurbita maxima*, seeds.

The association of the following families with the Cucurbitaceae is only possible on the morphological character afforded by the united anthers. A real relationship must not therefore be assumed, especially since the investigations of KRATZER have shown how various is the course of development of the seeds. There was, however, no better place in this short systematic account to treat of the very isolated Cucurbitaceae.

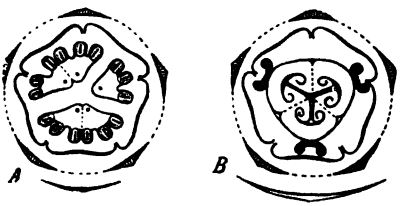


FIG. 773.—*Ecballium* (Cucurbitaceae). Diagrams of (*A*) a male and of (*B*) a female flower. (After EICHLER.)

Family 2. **Campanulaceae.**—Herbs with milky juice; flowers actinomorphic; ovary as a rule trilocular or pentalocular. The stamens are inserted on the floral axis and have their anthers joined together. The genus *Campanula* (Figs. 775, 776) has a number of British species with blue bell-shaped flowers. *Phyteuma* has spike-like inflorescences, the petals only separate near the base. Only after the pollen which has been shed in the bud has been swept out by the hairs on the style ([39]) do the petals open and the arms of the stigma spread apart. *Jasione* has capitulate inflorescences resembling those of Compositae.

Family 3. **Lobeliaceae** differ from the Campanulaceae in the zygomorphic flowers and two carpels. The median sepal is anterior and comes below a deep

incision in the corolla. The normal position is assumed by torsion of the whole

FIG. 774.—*Citrullus colocynthis* (½ nat. size). *1*, Shoot with male and female flowers. *2*, Apex of a shoot with a male flower-bud and tendrils. *3*, Male flower with corolla spread out. *4*, Female flower cut through longitudinally. *5*, Young fruit cut transversely. OFFICIAL.

flower through 180° or inversion of the flower (Fig. 777). In Britain *Lobelia Dortmanna*, an aquatic plant of northern regions, has a similar habit to *Litorella*.

OFFICIAL.—*Lobelia inflata* from N. America (Fig. 778) yields LOBELIA.

Family 4. Compositae.—Distributed over the whole earth. For the most part herbs of very various habit; some tropical forms are shrubs or trees, *e.g. Senecio Johnstoni.* The flowers are associated in

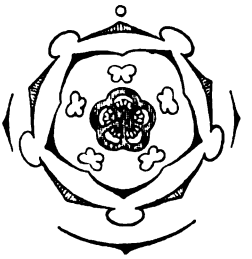


FIG. 775.—Floral diagram of *Campanula medium.* (After EICHLER.)

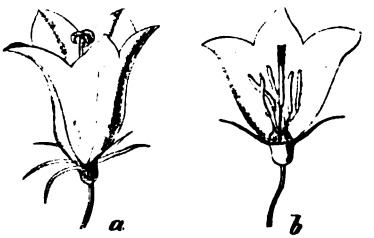


FIG. 776.—*Campanula rotundifolia.* *a*, Flower; *b*, the same cut through longitudinally. (Nat. size.) (After H. SCHENCK.)

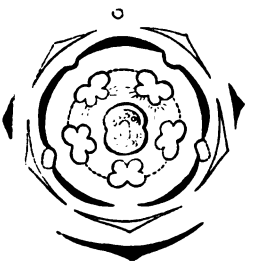


FIG. 777.—Floral diagram of *Lobelia fulgens.* (After EICHLER.)

FIG. 778.—*Lobelia inflata.* Upper portion of plant with flowers and fruits.

heads. The single flowers are actinomorphic or zygomorphic. Stamens five; anthers introrse, cohering by their cuticles to form a tube (Fig. 779) which is closed below by the unexpanded stigma. The pollen is shed into the tube formed by the anthers and is swept out by the brush-like hairs of the style as the latter elongates. The

style is bifid above. Ovule erect, anatropous (Fig. 780). Seed exalbuminous. The fruits are achenes, often bearing at the upper end a crown of hairs, the pappus. This corresponds to the calyx and aids in the dispersion of the fruit by the wind (Figs. 780, 785). As a reserve material in roots and tubers (Fig. 205) inulin as a rule is found; in the seeds aleurone grains and fatty oil.

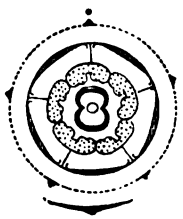


FIG. 779.—Compositae. Floral diagram (*Carduus*).

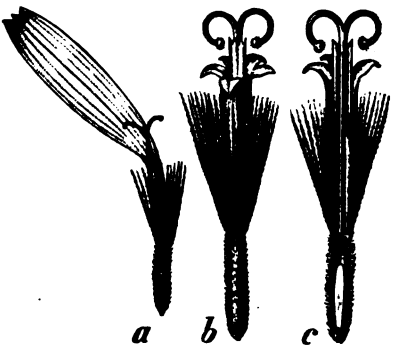


FIG. 780.—*Arnica montana*. *a*, Ray-flower; *b*, disc-flower; *c*, the latter cut through longitudinally. (After BERG and SCHMIDT, magnified.)

The individual flowers are either radially symmetrical with a five-lobed corolla (Fig. 780, *b*, *c*) or they are two-lipped as in the South American Mutisieae, the upper lip having two teeth, the lower three. By suppression of the upper lip

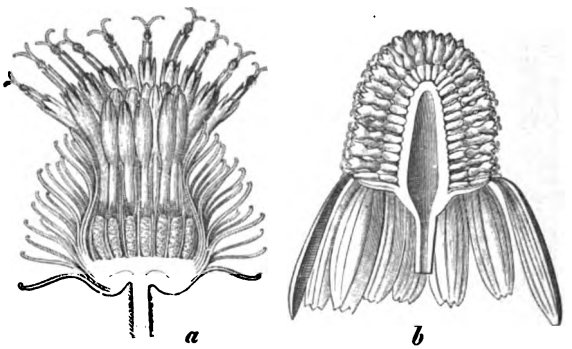


FIG. 781.—Longitudinal section of capitulum—*a*, of *Lappa major* with floral bracts; *b*, of *Matricaria Chamomilla* without floral bracts. (After BERG and SCHMIDT, magnified.)

flowers with a single lip are derived; such flowers exhibit three teeth at the tip (Fig. 780 *a*). The ligulate flowers (*e.g.* of *Taraxacum*) are similar in general appearance to the latter; the corolla is here deeply split on one side and its margin bears five teeth. In addition to those Compositae which have only ligulate or only tubular florets in the head, there are many which have tubular florest (disc-florets) in the centre, surrounded by one-lipped florets (ray-florets). These

usually differ from one another in sex as well as in colour; the disc-florets are hermaphrodite, the ray-florets purely female. The flower-heads are thus heterogamous (*Matricaria*, *Arnica*). Lastly, the marginal florets may be completely sterile (*Centaurea cyanus*) and serve only to render the capitulum conspicuous to insects.

One series of genera has only tubular florets in the head. *Carduus* (Plumeless Thistle), pappus of simple, hair-like bristles (Fig. 783). *Cirsium*, with feathery pappus. *Echinops*, with single-flowered capitula associated in numbers. *Lappa* (Burdock),

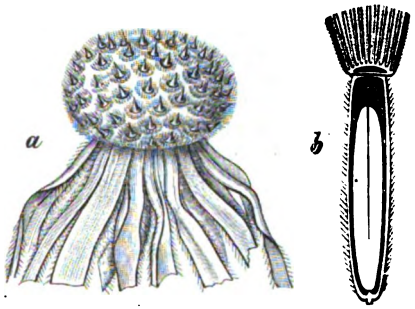


FIG. 782.—*Arnica montana*. *a*, Receptacle of capitulum after removal of fruit; *b*, fruit in longitudinal section, the pappus only partly shown. (After BERG and SCHMIDT, magnified.)

FIG. 788. — Androecium of *Carduus crispus* (× 10). (After BAILLON.)

involucral bracts with recurved, hook-like tips (Fig. 781 *a*). *Cynara Scolymus* (Artichoke). *Cnicus benedictus* (Fig. 786), capitula solitary, terminal, surrounded by foliage leaves. Involucral bracts with a large, sometimes pinnate, terminal

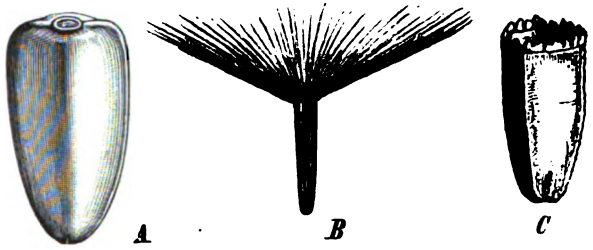


FIG. 784.—Fruits of—*A*, *Helianthus annuus*; *B*, *Hieracium virosum*; *C*, *Cichorium Intybus*. (After BAILLON.)

spine and a felt of hairs. *Centaurea* with dry, scaly, involucral bracts and large, sterile, marginal florets.

Other genera have only hermaphrodite ligulate florets in the capitulum, and have latex in all parts of the plant. *Taraxacum officinale* (Dandelion) is a common plant throughout the northern hemisphere. It has a long tap-root,

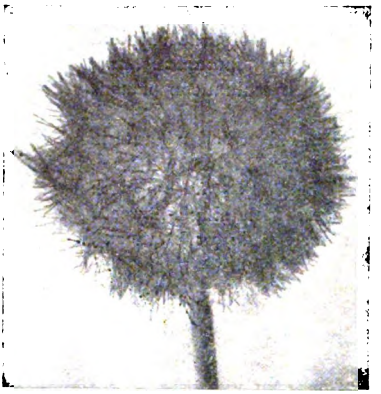


FIG. 785.—Head of fruits of *Taraxacum officinale*. The pappus is raised above the fruit on an elongated stalk. (Nat. size.)

FIG. 786.—*Cnicus benedictus*. (After BAILLON.)

a rosette of coarsely-toothed leaves, and inflorescences, borne singly on hollow

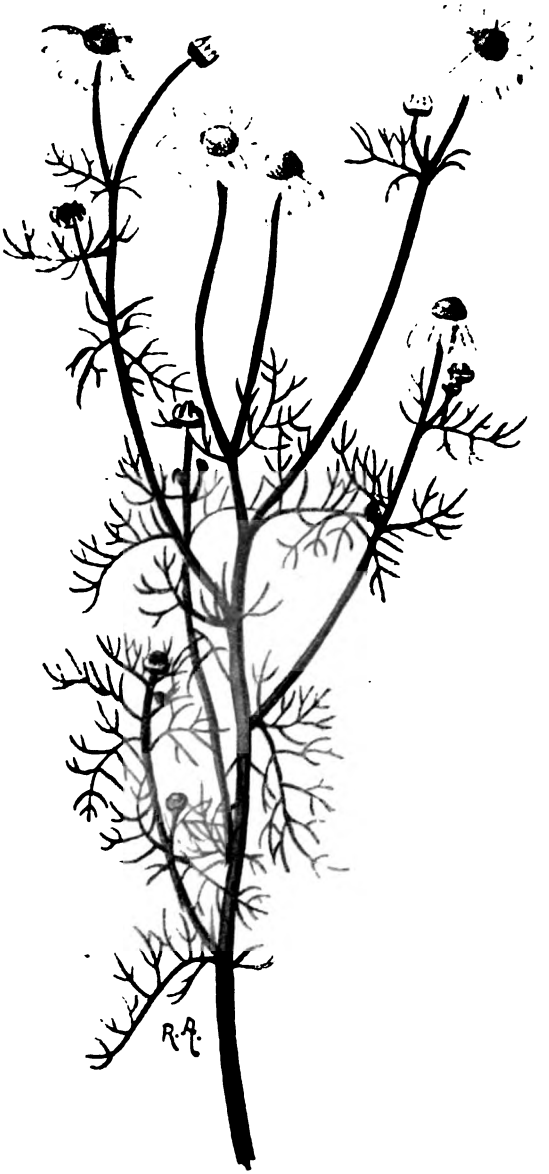


FIG. 787.—*Matricaria Chamomilla* (½ nat. size).

FIG. 788.—*Artemisia Cina*. (After SCHUMANN and ARTHUR MEYER.)

stalks; after flowering these exhibit a second period of growth (p. 281) (40).

Fruits with an elongated beak, carrying up the pappus as a stalked, umbrella-shaped crown of hairs (Fig. 785). *Lactuca sativa*, Lettuce. *L. virosa*. *L. Scariola*, Compass plant, has leaves which take a vertical position (cf. p. 351). *Cichorium Intybus* (Chicory) has blue flowers and a pappus in the form of short, erect scales (Fig. 784 *C*). *C. endivia*, Endive. *Tragopogon* and *Scorzonera* have a feathery pappus; *Sc. hispanica*. *Crepis* has a soft, flexible, hairy pappus of

FIG. 789.—*Tussilago Farfara*. (After BAILLON.)

brownish colour. *Sonchus*, pappus of several series of bristles. *Hieracium*, a large European genus with many forms. Pappus white, rigid, and brittle (Fig. 784 *B*).

Usually there are florets of two distinct types in the capitulum. Numerous species of *Aster*, *Solidago*, and *Erigeron* occur in Europe, America, and Asia. Species of *Aster* are cultivated. Species of *Haastia* and *Raoulia* are cushion-shaped plants with woolly hairs in New Zealand (Vegetable Sheep) (Fig. 191). *Inula* occurs in Britain; involucral leaves frequently dry and membranous. In *Gnaphalium*, *Antennaria*, *Helichrysum* (Everlasting flowers), *Leontopodium*

(Edelweiss), *Filago*, etc., the dry involucral bracts are coloured. *Helianthus annuus* (Sunflower, Fig. 784 *A*), *H. tuberosus* (Jerusalem Artichoke). *Dahlia*, from America and in cultivation. In Britain *Bidens*; herbs with opposite

FIG. 790.—*Arnica montana* (½ nat. size). OFFICIAL.

leaves, sometimes heterophyllous. *Achillea*, Milfoil; *A. moschata* and *A. atrata* are corresponding species of the Alps, the one on limestone and the other on schists. *Anthemis nobilis*, capitula composed of disc-florets only, or with these more or

less replaced by irregular florets. *Anacyclus officinarum*. *Matricaria Chamomilla* (Chamomile, Figs. 781 *b*, 787) is an annual copiously-branched herb with a hollow, conical, common receptacle, yellow disc-florets and white, recurved, female ray-florets, in the terminal capitula. *Chrysanthemum*, *C. segetum*. *Tanacetum*, flowers all tubular, marginal florets female. *Artemisia* has all the florets tubular and usually the peripheral ones female (*A. Absinthium*, Wormwood); in the few-flowered capitula of *A. Cina* (Fig. 788) all the florets are hermaphrodite.

Tussilago Farfara, Coltsfoot, flowers appear before the leaves; the flowering stem bears scaly leaves and a single capitulum (Fig. 789); the flowers stand on a smooth receptacle and have a fine white hairy pappus. Female flowers at periphery in several series. Leaves large, cordate, thick, covered beneath with white hairs. *Petasites officinalis*, Butter-Bur. *Senecio*, plants of diverse habit, including some trees and succulent plants; of world-wide distribution. *S. vulgaris* has no ray-florets but only tubular hermaphrodite florets. *Doronicum*, *Cineraria* are commonly cultivated. *Arnica montana* (Figs. 780, 782, 790) has a rosette of radical leaves in two to four opposite pairs and a terminal inflorescence bearing a single capitulum: from the axillary buds of the two opposite bracts one (rarely more) lateral inflorescence develops. *Calendula* and *Dimorphotheca* have the fruits of the capitulum of varied and irregular shapes.

OFFICIAL.—*Anacyclus Pyrethrum* yields PYRETHRI RADIX. SANTONINUM is prepared from *Artemisia maritima*, var. *Stechmanniana*. *Anthemis nobilis* yields ANTHEMEDIS FLORES. *Taraxacum officinale*, TARAXACI RADIX. *Arnica montana*, ARNICAE RHIZOMA. *Grindelia camporum*.

SUB-CLASS II

Monocotylae

The Monocotyledons, or Angiosperms which possess a single cotyledon, are in general habit mostly herbaceous, less frequently shrubs or trees.

In germination the radicle and hypocotyl of the small embryo emerge from the seed coat, while the sheath-like cotyledon usually remains with its upper end within the seed and absorbs the materials stored in the endosperm, which is usually well developed. The growth of the main root is sooner or later arrested and its place taken by numerous adventitious roots springing from the stem. In the Grasses these are already present in the embryo within the seed. Thus a single root system derived by the branching of a main root, such as the Gymnosperms and Dicotyledons possess, is wanting throughout the Monocotyledons.

The growing point of the stem remains for a longer or shorter time enclosed by the sheath of the cotyledon. Later it bears in two-ranked or alternate arrangement the leaves, which have long sheaths and continue to grow for a considerable time at their bases. The growth of the stem is often limited; branching is in many cases entirely wanting, and rarely results in the development of a highly branched shoot-system. The leaves are mostly sessile and parallel-veined, and of a narrow, elongated, linear, or elliptical shape

(Fig. 791). The pinnate or palmate leaves of the Palms and the perforated leaves of some Araceae are due to the perishing of definite portions of the lamina during development.

Anatomically the Monocotyledons are characterised by their closed vascular bundles in which no cambium is developed; these are uniformly scattered in the cross-section of the stem (cf. Fig. 109).

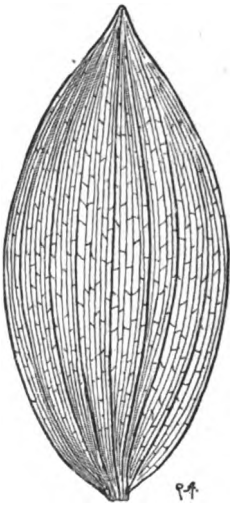


FIG. 791.—Leaf of *Polygonatum multiflorum* with parallel venation (½ nat. size).

FIG. 792.—Diagram of a typical Monocotyledonous flower.

Secondary thickening is consequently wanting in Monocotyledons, and in the rare cases in which it is found results from the formation at the periphery of the central cylinder of additional closed bundles embedded in ground-tissue (cf. p. 142).

The flower in the Monocotyledons is usually pentacyclic and has two whorls constituting the perianth, an androecium of two whorls, and a gynaeceum of a single whorl. The typical number of members in each whorl is three. The two whorls of the perianth are usually similarly formed and thus constitute a perigone (Fig. 792). The floral formula of such a flower is P 3 + 3, A 3 + 3, G (3).

(*a*) *Flowers actinomorphic*

Order 1. Helobiae

This order includes only aquatic or marsh plants. The radial or actinomorphic flowers have the gynaeceum frequently apocarpous and composed of two whorls of carpels, which develop into indehiscent fruitlets or follicles. Seeds exalbuminous; embryo large. The order connects by its floral structure the Monocotyledons with the Polycarpicae (cf. p. 630) ([14]).

Family 1. **Alismaceae.** — Widely spread in the warm and temperate zones. *Alisma Plantago*, *Sagittaria sagittifolia*, and *Butomus umbellatus* have long-

stalked panicles or umbels, and occur as marsh plants. The individual flowers

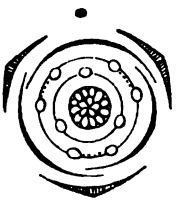


FIG. 793.—Floral diagram of *Echinodorus parvulus*, one of the Alismaceae. (After EICHLER.)

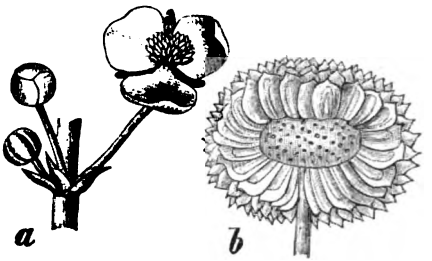


FIG. 794.—*Sagittaria sagittifolia*. *a*, Flower; *b*, fruit after removal of some of the carpels. (Magnified; *b*, after ENGLER and PRANTL.)

have a calyx and a white (in *Butomus*, reddish) corolla. Androecium, with six or

FIG. 795.—*Potamogeton natans*. Flowering shoot. (½ nat. size.)

more stamens. Gynaeceum apocarpous, with six or many carpels that may be in whorls or spirally arranged (Fig. 793). *Sagittaria* is monoecious with flowers that,

by suppression of stamens or carpels, are unisexual. Male flowers, with numerous stamens and sterile carpels; female flowers, with staminodes and numerous free carpels inserted on the convex floral receptacle (Fig. 794). Leaves in *Butomus*, linear, channelled, and triangular in cross-section; in *Alisma* and *Sagittaria*, long-stalked with spoon-shaped and sagittate leaf-blades respectively. Individuals of both genera growing in deep flowing water have long ribbon-shaped leaves, similar to those that appear as a transition type in germination; such plants do not flower.

Family 2. **Potamogetonaceae.**—Many species of *Potamogeton* are distributed over the earth in standing or flowing water. Leaves usually submerged, with a long sheath, slit on one side, formed from the axillary stipules. *P. natans*, the common Pond-weed (Fig. 795), at the time of flowering has usually only floating leaves, the cylindrical, submerged water-leaves having disappeared by then. *Ruppia maritima* and *Zanichellia palustris* grow in brackish water. *Zostera marina*, Grass-wrack, occurs commonly on all north temperate coasts and is used for stuffing cushions.

Family 3. **Hydrocharitaceae.**—*Hydrocharis morsus ranae* and *Stratiotes aloides* are floating plants occurring in Britain, which are vegetatively propagated by runners; they pass the winter at the bottom of the water, in some cases as special winter buds, and grow up again in the spring. Flowers dioecious; entomophilous. The male flower has several trimerous whorls of stamens; the female flower possesses staminodes and two trimerous whorls of carpels. *Vallisneria spiralis*, a fresh-water plant of the tropics extending to the Italian lakes. *Elodea canadensis*, the Canadian water-weed (hydrophilous, cf. p. 553).

Order 2. Liliiflorae

Flowers actinomorphic, composed of five whorls, with superior or inferior ovary. Both whorls of the perianth developed alike (Fig. 792). Only in the Iridaceae is one whorl of the androecium suppressed. The gynaeceum varies in position, but it is always formed of three carpels and in most cases has a trilocular ovary.

FIG. 796.—*Juncus lamprocarpus*. *a*, Part of an inflorescence; single flower (*b*) and gynaeceum (*c*) magnified.

Family 1. **Juncaceae.**—Plants of grass-like habit. Flower of complete Liliaceous type; with scaly perianth. Wind-pollination. Pollen grains united in tetrads. Ovary superior, uni- or trilocular, bearing three long papillose stigmas. Endosperm floury. Fruit a capsule. Distributed in the temperate zones of both hemispheres.

Numerous species of *Juncus* (Rush) occur in our flora, in marshy ground; the leaves are cylindrical and have large intercellular spaces. The clusters of small anemophilous flowers (Fig. 796) are borne on the end of a shoot, but are often displaced to the side by the bract which continues the line of the axis. Fruits with

FIG. 797.—*Colchicum autumnale* (½ nat. size). *f*, Fruit in transverse section; *g*, seed with embryo (*e*) (enlarged). *POISONOUS* and *OFFICIAL*.

FIG. 798.—*Urginea scilla* (about $\frac{1}{10}$ nat. size). *OFFICIAL.* (After BERG and SCHMIDT.)

FIG. 799.—*Ornithogalum umbellatum*. *a*, Entire plant (reduced); *b*, flower (nat. size); *c*, flower, part of perigone and androecium removed; *d*, fruit; *e*, fruit in transverse section. (*c-e* magnified.)

many seeds. *Luzula*, with flat leaves and three-seeded fruits, one of the earliest spring-flowering plants.

Family 2. **Liliaceae.**—Typical flower, with coloured, conspicuous perianth. Entomophilous. Ovary superior. The fruits are septicidal

FIG. 800.—*Aloë speciosa* and *Aloë ferox*. With, in the latter, branched inflorescences. (After MARLOTH.)

or loculicidal capsules, or berries. Seeds numerous. Endosperm horny or fleshy.

The majority of the Liliaceae are perennial herbs with bulbs, tubers, or rhizomes. They mainly inhabit the warm temperate regions. *Colchicum autumnale*, the Autumn Crocus (Fig. 797), is a perennial herb growing in meadows. If a plant is examined in autumn at the time of flowering, the corm (*k*), to the base of which is attached the lateral shoot bearing the flowers, will be seen to be enclosed in a brown envelope. The lateral flowering shoot bears at its base three sheathing

leaves not separated by elongated internodes. In the axil of the third of these is a bud which will form the flowering shoot of the next season. In spring the reserve materials from the corm are absorbed and the old corm is pushed aside by the swollen internode which in its turn enlarges to form a new corm. The three foliage leaves expand their long, channelled, dark green laminae above the soil; their sheathing portions closely surround the axis. The latter bears the fruits, which contain numerous, spherical, black seeds; these are liberated by the dehiscence of the capsule at the sutures (Fig. 797 *f*). *Veratrum album* is a conspicuous herb with a rosette of large, elliptical, longitudinally-folded leaves. The growth of the main axis is terminated by an inflorescence, which is a panicle more than a metre in height; the leaves borne on it have long sheaths and diminish in size from below upwards. The greenish-white flowers are polygamous. *Schoenocaulon* (*Sabadilla*) *officinale*, a bulbous plant of the Andes with grass-like leaves, has also septicidal capsules.

Such popular flowers as *Tulipa* (Fig. 204), *Hyacinthus*, *Lilium* (Fig. 207), *Muscari*, and *Scilla*, and vegetables as *Allium*, together with *Urginea* (Fig. 798), which occurs in the Mediterranean region, have on the other hand, without exception, loculicidal capsules. *Ornithogalum umbellatum* (Fig. 799 *a-e*) will serve as an example of this group. In autumn the plant consists of a bulb, each of the fleshy scales of which has a scar at the upper end. In the axil of the innermost scale is the stalk of the spent inflorescence together with a young bud bearing a number of leaves. Each of these leaves is provided with an embryonic lamina, while the continuation of the shoot is the embryonic inflorescence. In spring the leaves grow into long linear structures, and, together with the inflorescence, appear above ground. The inflorescence is sparingly branched; the white flowers have a trilocular ovary bearing a common style. The upper parts of the leaves wither, while the basal portions become swollen and fleshy and stored with reserve materials; the scar at the upper part of each scale marks the place of separation of the leaf-blade. The annual course of development is essentially similar in other bulbous plants. The vegetative period is restricted to a few months, while during the cold or, in the numerous bulbous plants of warm-temperate climates, the dry seasons, the bulb is protected by its subterranean situation. *Aloë*, a genus of African plants containing many species (Figs. 800, 801), has succulent leaves with spiny margins.

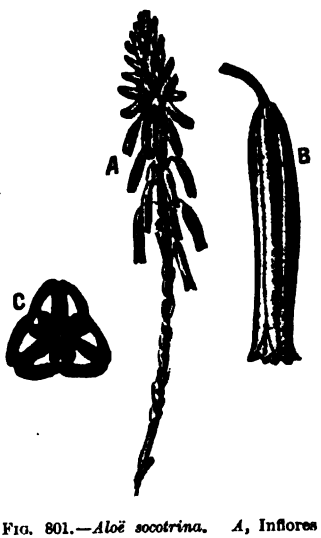


FIG. 801.—*Aloë socotrina*. *A*, Inflorescence. *B*, Flower. *C*, Ovary in cross-section.

Dracaena (Fig. 802), an arborescent form which attains a great age and a characteristic appearance, together with the similar genera, *Cordyline* and *Yucca*, and *Smilax* (Sarsaparilla), a shrubby plant of warmer countries, climbing by the help of tendril-like emergences at the base of the petioles, have berries. Other examples are *Asparagus* with bunches of phylloclades in place of leaves, *Convallaria* (Fig. 123), *Maianthemum*, *Polygonatum* (Fig. 138), and *Paris quadrifolia* (Fig. 803); the latter bears whorls of four leaves, sometimes 3-6 leaves ([41])

All these plants have creeping rhizomes bearing scale-leaves; either the apex of this rhizome grows annually into the erect shoot bearing the foliage leaves and inflorescences, while the growth of the rhizome is continued by a lateral branch (*Polygonatum*), or the rhizome continues its subterranean growth, the leafy shoots being developed from axillary buds (*Paris*).

POISONOUS.—Numerous Liliaceae are more or less poisonous, *e.g.* Lily of the Valley, Tulip, *Fritillaria*, *Colchicum*, *Veratrum*, *Paris*.

OFFICIAL.—*Colchicum autumnale*, seeds and corm. *Aloë vera*, *A. chinensis*, *A. perryi*, and other species yield ALOËS BARBADENSIS and ALOËS SOCOTRINA. *Urginea scilla* yields SQUILL. *Urginea indica*.

FIG. 802.—*Dracaena draco*. The Dragon Tree of Laguna in the Canary Islands. (After CHUN.)

Family 3. **Amaryllidaceae.**—Distinguished from Liliaceae by the inferior ovary. Mostly tropical and sub-tropical. *Leucojum* (Fig. 804), the Snowdrop (*Galanthus*), and *Narcissus* resemble the bulbous Liliaceae in habit. The majority of the genera belong to the tropics or sub-tropics, *e.g. Haemanthus*, *Clivia*, *Crinum*, species of which are often grown in greenhouses. *Agave*, large plants with succulent leaves from the warmer regions of America, provide fibres. *Agave Sisalana* from Yucatan, one of the most important fibre-yielding plants, is extensively cultivated in East Africa and other colonies with dry and warm climates. *A. salmiana* provides the national drink of Mexico (pulque), obtained by fermenting the sap that flows on cutting off the inflorescence. Species of *Agave* are acclimatised in the Mediterranean region.

Family 4. **Iridaceae.**—Distinguished from Liliaceae by their inferior ovary and by the suppression of the inner whorl of the

androecium (Fig. 805). The two whorls of the perianth are not

FIG. 803.—*Paris quadrifolia* (½ nat. size). *POISONOUS.*

always similar. Anthers extrorse. The leaves of the Iridaceae are

always sessile; the underground portion is a tuberous or elongated rhizome, less commonly a bulb. Capsule loculicidal. This family is mainly represented in the Cape and the warmer parts of America.

FIG. 804. — *Leucojum aestivum*. *a*, Inflorescence (reduced); *b*, gynaeceum and androecium (nat. size). (After SCHIMPER.)

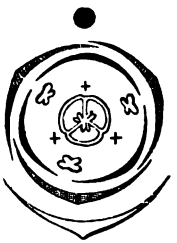


FIG. 805.—Floral diagram of the Iridaceae (*Iris*). (After SCHENCK.)

FIG. 806.—*Crocus sativus*. Style with tripartite stigma. (After BAILLON.)

Crocus sativus, Saffron (Fig. 806), is a plant which has long been cultivated in the East; it has a tuberous rhizome and narrow, grass-like leaves. The flowers are sterile unless pollinated with pollen of the wild form. The large stigmas

FIG. 807.—*Iris germanica* (⅓ nat. size).

furnish Saffron. Other species are cultivated as ornamental plants. *Iris*, leaves overlapping in two ranks. The leaf-sheath surrounds the thick fleshy rhizome, while the sword-shaped blade stands erect and has its two lateral surfaces alike (Fig. 807). Outer perianth segments bent downwards, inner erect. The three anthers are roofed over by the three leaf-like styles. In *Gladiolus* the flowers are dorsiventral, and the dissimilarity of the perianth leaves is more marked.

Family 5. **Bromeliaceae.**—Mostly epiphytes; flowers hermaphrodite. Limited to tropical and sub-tropical parts of America. The leaves are in rosettes and are typically xerophytic; in the forms which grow in the soil they are spiny. *Ananassa sativa* is cultivated; its inflorescence forms the Pineapple.

Order 3. Enantioblastae

Characterised by the atropous ovules; the embryo is at the summit of the endosperm at the opposite end from the hilum.

Family. **Commelinaceae.** Tropical and sub-tropical. Perianth developed as calyx and corolla. *Commelina, Tradescantia.* The hairs of the stamens afford well-known objects for the study of movements of protoplasm and nuclear divisions.

(*b*) *Flowers more or less reduced*

Order 4. Glumiflorae

This order consists entirely of annual or perennial plants of grass-like habit. It is distributed over the whole surface of the earth. A woody stem only appears in the genus *Bambusa.* The association in more or less complex inflorescences of numerous flowers, which lack a proper perianth but are enclosed by scaly bracts (glumes), is a common character of the order. The perianth is either completely wanting or reduced to a series of scales or bristles. The inner whorl of stamens is also usually wanting. The superior ovary is always unilocular and contains only one ovule; it is formed of three (Cyperaceae), two (some Carices), or of a single carpel (Gramineae). The large size and feathery and papillose form of the stigmas stand in relation to the wind pollination. Fruits indehiscent.

Family 1. **Cyperaceae.**—The Sedges are characterised by their triangular stems, which are usually neither swollen at the nodes nor hollow, and by their closed leaf-sheaths. The flowers are unisexual and then usually monoecious (*Carex*) or are hermaphrodite as in the majority of the genera; ovary formed of two or three carpels with an erect, basal, anatropous ovule. Pericarp not coherent with the seed-coat; embryo small, surrounded by the endosperm.

The genera *Cyperus*, *Scirpus*, and *Eriophorum* have hermaphrodite flowers. Fig. 808 represents a plant of *Scirpus setaceus*, which is an annual, in flower. Leaves rigid, channelled above. Fertile shoots with the uppermost internode elongated. Spikes 1-3, terminal; enclosed by imbricating bracts and displaced to one side by the subtending bract, the line of which continues that of

the stem. Only the large lowermost bracts are sterile, the others have each a naked hermaphrodite flower in their axils. The Cotton-grass (*Eriophorum angustifolium*), which when flowering is inconspicuous, bears at the summit of its fertile shoots 3-7 long-stalked erect spikelets with numerous imbricate bracts. Around the base of each flower are numerous hairs, which are concealed by the projecting stamens and style. When the plant is in fruit the hairs, which have become about 3 mm. long, project freely from between the bracts and constitute a valuable means of dispersal for the fruits. The white colour of the hairs makes

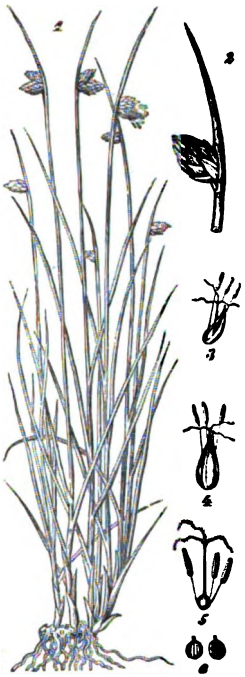


FIG. 808.—*Scirpus setaceus*. *1*, plant in flower; *2*, upper portion of a flowering shoot; *3*, single flower; *4*, the same from behind; *5*, the same without the bract; *6*, fruit. (*1*, nat. size, the others × 2-6. After HOFFMANN.)

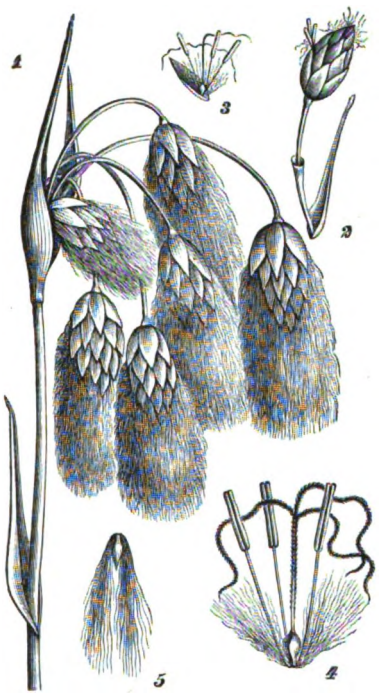


FIG. 809.—*Eriophorum angustifolium*. *1*, Inflorescence; *2*, a single spikelet; *3*, single flower; *4*, flower with bract removed; *5*, fruit. (*1*, about nat. size, the others × 3-5. After HOFFMANN.)

the now pendulous spikelets of the Cotton-grass a conspicuous feature of peat-moor vegetation (Fig. 809). *Cyperus papyrus*, in Egypt and Sicily, provided from its stems, which are as thick as the thigh, the "paper" of the ancient Papyri.

The genus *Carex* is for the most part monoecious, and its flowers are naked and unisexual. Male spikes simple; in the axil of each bract is a male flower formed of three stamens (Fig. 810 *A*). The female spikes bear in the axil of each bract a secondary shoot; the axis of this is included in the tubular subtending bract (utriculus) together with the pistil (formed of 2 or 3 carpels), which is borne in the axil of the bract (Fig. 810 *B-E*).

Family 2. **Gramineae** (42).—The stems of the true Grasses are cylindrical, and have hollow internodes (exceptions Maize and Sugar-cane); the nodes are swollen; the leaves are two-ranked and their sheath is usually split and thickened at the node. At the junction of the sheath and leaf-blade a membranous structure (the ligule) projects (cf. Fig. 133). The flowers of the Gramineae are grouped in spicate, racemose, or paniculate inflorescences, which are always composed of partial inflorescences, the spikelets. Usually each SPIKELET bears several flowers. At the base of the spikelet there are usually (Fig. 811) a pair of sterile bracts (GLUMAE); sometimes there is only one or 3-4 glumes. Continuing the two-ranked arrangement of the

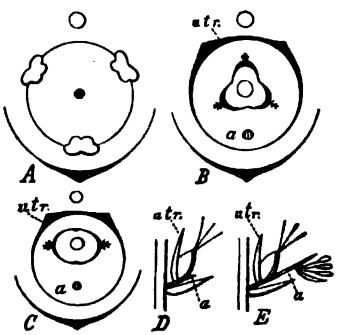


FIG. 810.—*A*, Floral diagram of a male flower of *Carex*; *B*, of a female flower with three stigmas; *C*, of a female flower with two stigmas. *D*, Diagram of female flower of *Carex*. *E*, Diagram of the hermaphrodite spikelet of *Elyna*; *a*. secondary axis; *utr*, utriculus or bract of the secondary axis. (After EICHLER.)

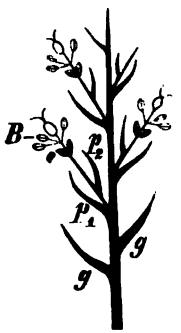


FIG. 811.—Diagrammatic representation of a Grass spikelet. *g*, The glumes; p_1 and p_2, the inferior and superior palea; *e*, lodicules; *B*, flower. The axial parts are represented as elongated.

glumes come the fertile subtending bracts (PALEA INFERIOR), in the axil of each of which stands a flower. The subtending bracts are often awned, *i.e.* they bear terminally or springing from the dorsal surface a stiff bristle with backwardly directed hairs (the AWN). The bracteole of each flower is represented by another scale-like bract, the PALEA SUPERIOR. Above this come two small scales, the LODICULAE, the distension of which assists in opening the flower (Fig. 812 *B*, *C*). Lastly, the axis bears the androecium consisting of a whorl of three stamens, and the ovary composed of one carpel and bearing two feathery papillose stigmas. The ovary contains an anatropous, or slightly campylotropous ovule.

The flowers do not always show such extreme reduction; thus the flower of Rice (Fig. 817) has a complete androecium; that of the Bambuseae is similar and also has three lodicules, and in *Streptochaeta* there is a normal monocotyledonous type of flower with all five whorls of members present and three carpels indicated

in the development of the ovary. The lodicules can on this evidence be regarded as corresponding to the inner whorl of the perianth. Possibly the superior palea represents two coherent leaves of the outer whorl. In the gynaeceum there remains as a rule only a double leaf formed of the two lateral carpels of the three originally present. According to this view, which we owe to GOEBEL, the diagram in Fig. 813 is arrived at.

On the wind-pollination of Grasses cf. p. 552. The fruit of the Grasses is termed a caryopsis; in it the pericarp and seed-coat are intimately united. The embryo lies in contact with the endosperm by means of its cotyledon; this forms the SCUTELLUM, and in germination serves as an absorbent organ by means of

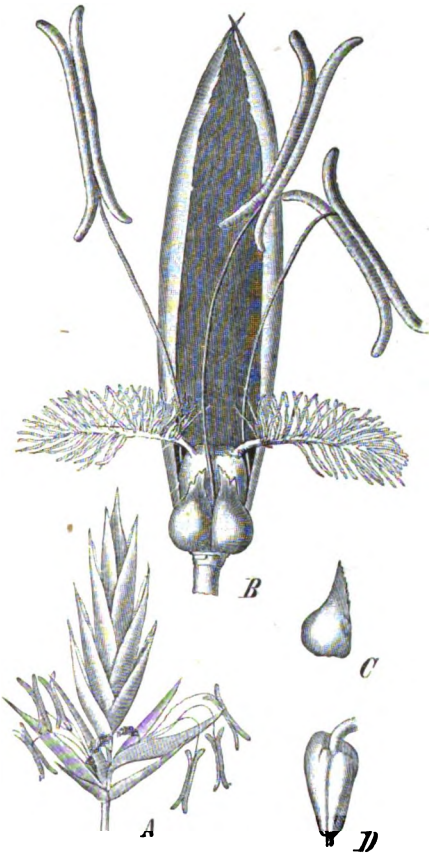


FIG. 812.—*Festuca elatior*. *A*, Spikelet (compare Fig. 811), with two open flowers below which the two sterile glumes are seen (×3). *B*, Flower; the two lodicules are in front, the superior palea behind; the ovary bears two feathery stigmas (× 12). *C*, A single lodicule (× 12). *D*, Ovary seen from the side with the stalk of one of the removed stigmas (× 12). (After H. SCHENCK.)

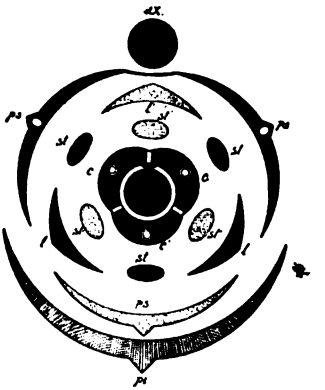


FIG. 813.—Diagram of the Grass flower. The missing parts are dotted; *ax*, end of the axis of the spikelet; *pi*, palea inferior; *ps*, palea superior (outer perigone); *l*, lodiculae (inner perigone); *st*, outer, *st'*, inner whorl of stamens; *c*, lateral carpels; *c'*, dorsal carpel. (After SCHUSTER.)

which the reserve materials in the endosperm are taken up by the seedling (Fig. 814).

The most important economic plants belonging to this order are the Cereals (Fig. 815). Wheat, *Triticum*. Spikelets single, with two or more flowers; glumes broadly ovate. KOERNICKE distinguishes as species of Wheat—(1) *Tr. vulgare*, with a number of sub-species; (2) *Tr. polonicum*; (3) *Tr. monococcum*. Rye, *Secale cereale*; spikelets single, 2-flowered; glumes acute. Barley, *Hordeum vulgare*;

spikelets one-flowered, in groups of three; in the sub-species *H. hexastichum* and *H. tetrastichum* all the rows of spikelets are fertile, in *H. distichum* only the middle row. Oat, *Avena sativa*. Maize, *Zea mais*. The above are all cultivated in temperate climates, the Maize largely in America, the others also in Western Asia and the south-east of Europe. In the wild state only *Triticum monococcum*, var. *aegilopodioides* (from which *Tr. monococcum* is derived), *Triticum dicoccoides* as the original form of Wheat, *Secale montanum*, and *Hordeum spontaneum* (allied to *H. distichum*) are known. In these wild forms the spikelets fall from the rachis at maturity, a character that would be unsuitable in cultivated forms.

The most important tropical food-plant of the order is Rice, *Oryza sativa* (Fig. 817), which is largely cultivated to the limits of the warmer temperate regions, and, when sufficient moisture is available, yields an enormous harvest (Fig. 818). In Africa several varieties of Millet, *Andropogon Sorghum*, are cultivated, and it

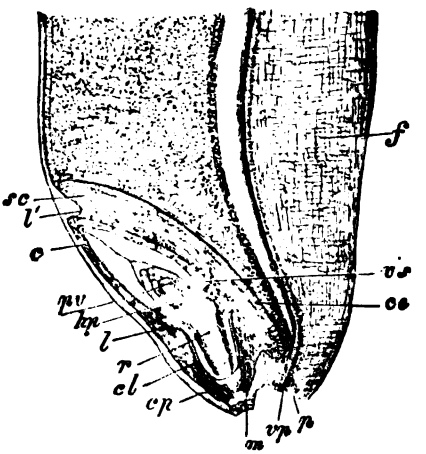


FIG. 814.—Part of median longitudinal section of a grain of Wheat, showing embryo and scutellum (*sc*); *vs*, vascular bundle of scutellum; *cc*, its columnar epithelium; *l'*, its ligule; *c*, sheathing part of the cotyledon; *pv*, vegetative cone of stem; *hp*, hypocotyl; *l*, epiblast; *r*, radicle; *cl*, root-sheath; *m*, micropyle; *p*, funiculus; *vp*, its vascular bundle; *f*, lateral wall of groove *cp*, pericarp. (× 14.) (After STRASBURGER.)

forms the most important cereal for that continent. *Panicum miliaceum* and *P. italicum*, of Asiatic origin, are still cultivated, though to a diminished extent, in the Mediterranean region. The Sugar-cane, *Saccharum officinarum*, is another important food-plant; it is a perennial, growing more than six feet high, and occurs in tropical Asia. The sugar-cane is cultivated in all tropical countries, and cane-sugar is obtained from the sap expressed from the solid stem.

Among the most important of our meadow-grasses may be mentioned *Agrostis alba*, *Alopecurus pratensis*, *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Avena flavescens*, *A. pubescens*, *Briza media*, *Dactylis glomerata*, *Holcus lanatus*, *Lolium perenne*, *Phleum pratense*, *Poa pratensis*, and species of *Aira*, *Bromus*, *Calamagrostis*, *Festuca*, *Melica*, etc. The tropical species of *Bambusa*, which grow to the height of trees, are utilised in many ways; from the stems are constructed houses, walls, flooring, ladders, bridges, cordage, water-vessels, cooking utensils, water-pipes, etc., and the plant is indispensable in the countries in which it occurs.

POISONOUS.—*Lolium temulentum* (Fig. 819) has its fruits sometimes infested with fungal hyphae. These fruits owing to the alkaloids they contain are poisonous, but fruits free from fungus are harmless (43); the plant is an annual, and can be

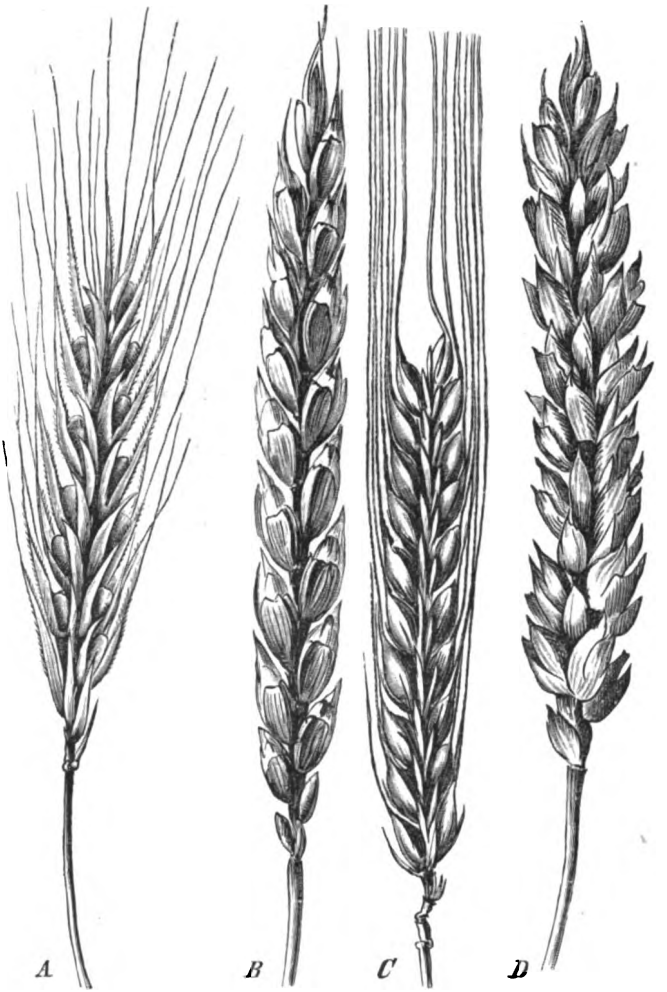


FIG. 815.—Cereals. *A*, Rye, *Secale cereale*. *B*, Spelt, *Triticum Spelta*. *C*, Two-ranked barley, *Hordeum vulgare, distichum*. *D*, Wheat, *Triticum vulgare*.

distinguished by the absence of sterile shoots from the common *Lolium perenne* and *L. multiflorum*.

OFFICIAL.—AMYLUM (starch) is obtained from *Triticum sativum*, *Oryza sativa*, *Zea mais*, etc.; *Agropyrum repens*.

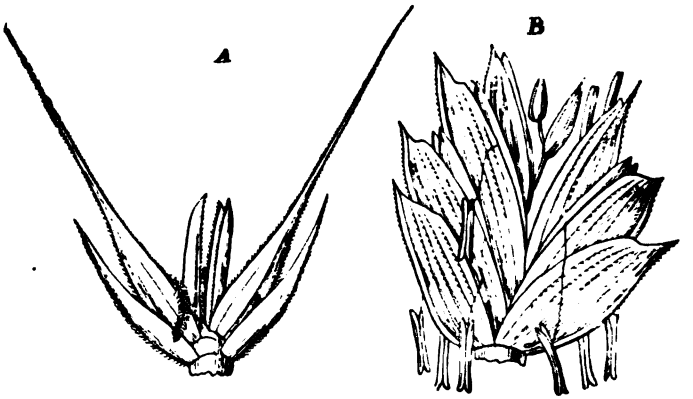


FIG. 816.—*A*, Spikelet of Rye; two-flowered. *B*, Spikelet of Wheat with a number of flowers.

FIG. 817.—*Oryza sativa*. Panicle (½ nat. size), and a single spikelet (enlarged).
OFFICIAL.

Order 5. Spadiciflorae

The common character of this order is afforded by the peculiar inflorescence; this is a spike with a thick, swollen, often fleshy axis and is termed a spadix. The flowers are mostly diclinous, monoecious, or more rarely dioecious.

Family 1. **Typhaceae.**—Marsh plants, with long, linear leaves and long-stalked spikes, which bear a large number of flowers, the male above, the female lower down. Perianth wanting.

FIG. 818.—Terraced land in Ceylon for the cultivation of Rice. The water required for the young plants flows from terrace to terrace through gaps in the boundary walls. In the foreground Bananas, and to the right a Coffee plantation. In the centre Areca palms. (From a photograph.)

Family 2. **Sparganiaceae.**—Connected with the preceding family. Spikes spherical. Flowers with a perigone, but otherwise like the Typhaceae.

Family 3. **Pandanaceae.**—Screw-pines. Trees of peculiar appearance, supported by prop-roots, or climbing shrubby plants; all belong to the tropical countries around the Indian Ocean and to the Pacific islands. Leaves elongated, spiny, channelled above, arranged without bare internodes in three ranks on the axis. Inflorescences, ♂ or ♀, are terminal spikes in the axils of sheathing bracts. Flowers without perianth, *Pandanus* (cf. Fig. 822 in front of the Palms), *Freycinetia* (cf. p. 558).

Family 4. **Palmae** (44).—The Palms are an exclusively tropical and subtropical family, the members of which mostly attain the size of trees. Their slender stem is simple and usually of uniform diameter throughout; only the African species of *Hyphaene* have branched stems. Other forms show evident growth in thickness towards the base and sometimes for half the height of the stem; this either depends on enlargement of the elements already present, or to a limited extent on new formation of tissues when required. The leaves, which are often of gigantic size, form a terminal crown. They are either pinnately or palmately divided, the division coming about by the death of definite portions of tissue in the young leaf in the bud, and subsequent tearing along these lines. The inflorescence is in some cases terminal (*Metroxylon*), and the individual perishes with the development of the fruits. More often the inflorescences are axillary. When young, they are enclosed by a massive resistant sheath, the spathe; this bursts open and permits of the unfolding of the simple, or more usually branched, inflorescence.

FIG. 819.—*Lolium temulentum*. POISONOUS. (After H. SCHENCK.)

The individual flowers are as a rule unisexual and constructed on the ordinary monocotyledonous type; P 3+3, A 3+3, in the male flowers, and P 3+3, G (3), in the female flowers. In *Cocos* their distribution is monoecious. Fig. 820 represents the inflorescence of *Cocos nucifera*, still partly enclosed by the spathe. The male flowers are crowded on the terminal branches of the inflorescence, while the female flowers are considerably larger and stand singly lower down. The ovary, which is here composed of three united carpels, becomes, as a rule, unilocular in the fruit, since only one carpel develops further. The ripe fruits are borne

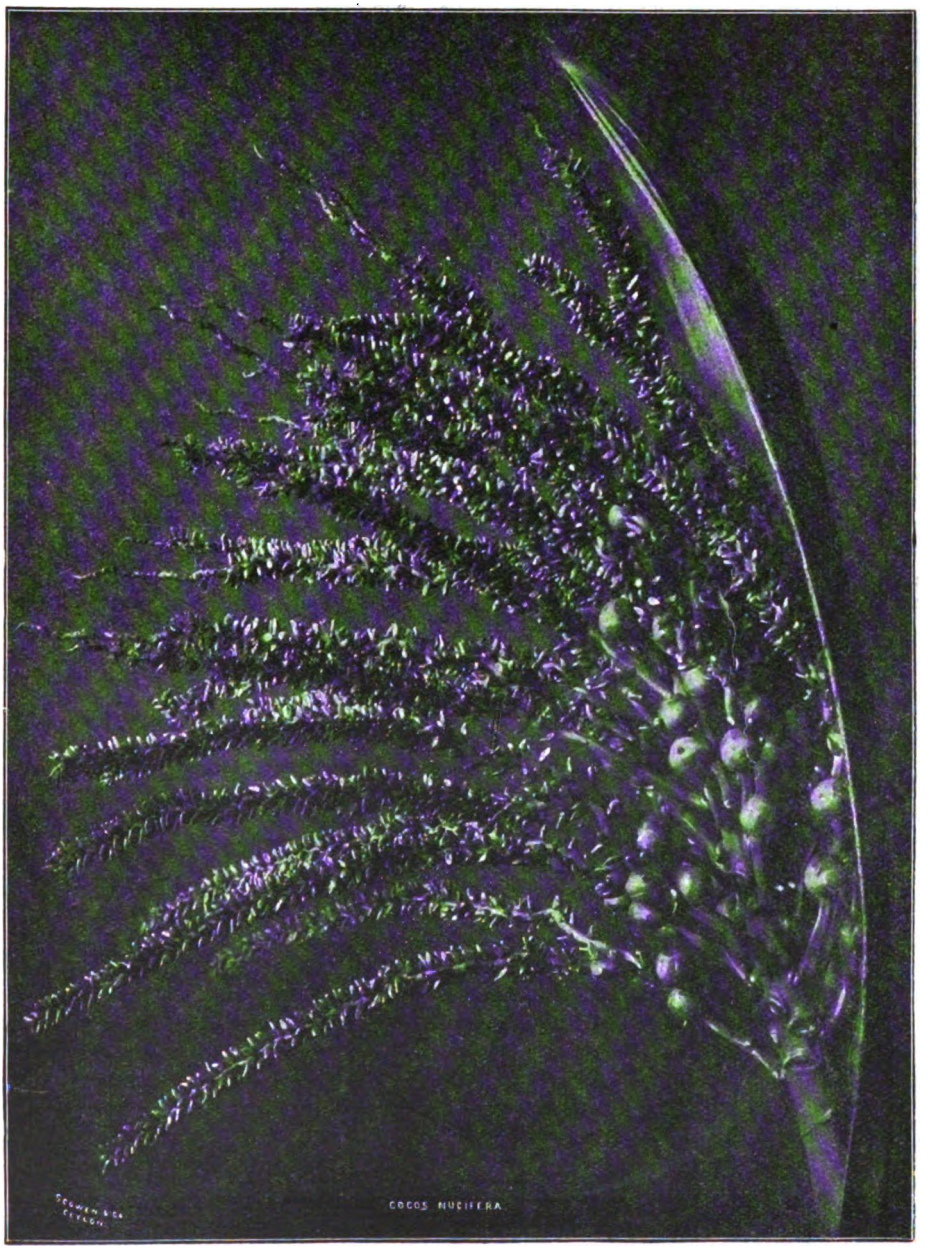


FIG. 820.—*Cocos nucifera.* Inflorescence of the Coco-nut Palm. (Greatly reduced.)

in small numbers on each inflorescence. Each consists of a coarse, fibrous exocarp, which contributes to the buoyancy of the fruit in water, and thus leads to the wide distribution of this palm on tropical coasts, and a hard endocarp. At the base of each carpel a germinal pore is present in the endocarp (Fig. 821), but only the one in relation to which the embryo lies remains permeable. The endosperm forms a thick layer within the endocarp; it is rich in fatty substances and produces the COPRA of commerce. The space within the endosperm is partially filled with fluid, the "milk" of the coco-nut, which is possibly of service in germination. The embryo on germination develops a massive absorbent organ which grows into the cavity of the fruit and serves to absorb the reserve materials. Fig. 822 shows the general habit of Coco-nut palms.

Differences are, however, found within the order. In *Areca catechu* (Fig. 818) the fruit developed from a similar ovary to that of *Cocos* is a berry, the exocarp becoming partly fibrous and partly succulent. The white endosperm is here of stony consistence, cellulose being stored as a reserve material; the endosperm is ruminated, *i.e.* the dark seed-coat grows into it at many points and gives it a veined appearance. The fruit of the Date Palm (*Phoenix dactylifera*) is also a berry, but this arises from one of the carpels of the apocarpous gynaeceum, the other two not developing. In contrast to the other genera mentioned, *Phoenix* is dioecious. Other important economic plants among the Palms are *Elaeis guineensis*, the African Oil Palm, species of *Calamus* which yield Malacca Cane, and species of *Metroxylon*, from which Sago is obtained; the two latter are found in the Asiatic-Australian region of the tropics. *Phytelephas macrocarpa*, an American Palm which does not form a trunk, yields vegetable ivory (the hard endosperm). Several species yield a flow of sugary sap on cutting off the inflorescence, and this is sometimes fermented to make Palm-wine and sometimes used as a source of cane-sugar (*Arenga saccharifera*).

FIG. 821.—Coco-nut after partial removal of the fibrous exocarp. (Reduced. After WARMING.)

Family 5. **Araceae.**—The Araceae are mostly herbs or shrubs; they take a conspicuous place as root-climbers in the damp tropical forests. The leaves of some species (*e.g. Monstera*) have the large lamina incised or perforated; this comes about by the death of definitely limited areas and is comparable to the method by which the leaves of Palms become compound. The flowers are greatly reduced, usually diclinous, borne on a swollen, fleshy axis; a spathe, often of bright colour and serving to render the inflorescence conspicuous, is present at the base of the spike (*e.g. Anthurium scherzerianum*, *Richardia aethiopica*, both of which are commonly cultivated). Fruit usually a red, bluish, or white berry.

Acorus calamus has, in the course of the last two or three centuries, spread to this country from the East. It has complete, hermaphrodite flowers; ovary trilocular. The short spadix is terminal, but is displaced to one side by the spathe which resembles the foliage leaves (Fig. 823).

POISONOUS.—Many Araceae are poisonous. *Calla palustris* in peaty swamps. *Arum maculatum* (Fig. 824), a perennial herb with tuberous rhizome, common in woods. It develops a number of stalked, hastate leaves, the brown spots on which give the plant its specific name. The flowers are monoecious, without perianth; the female flowers stand at the base of the spadix and the male a short distance above them. Above the latter come a number of sterile flowers with downwardly

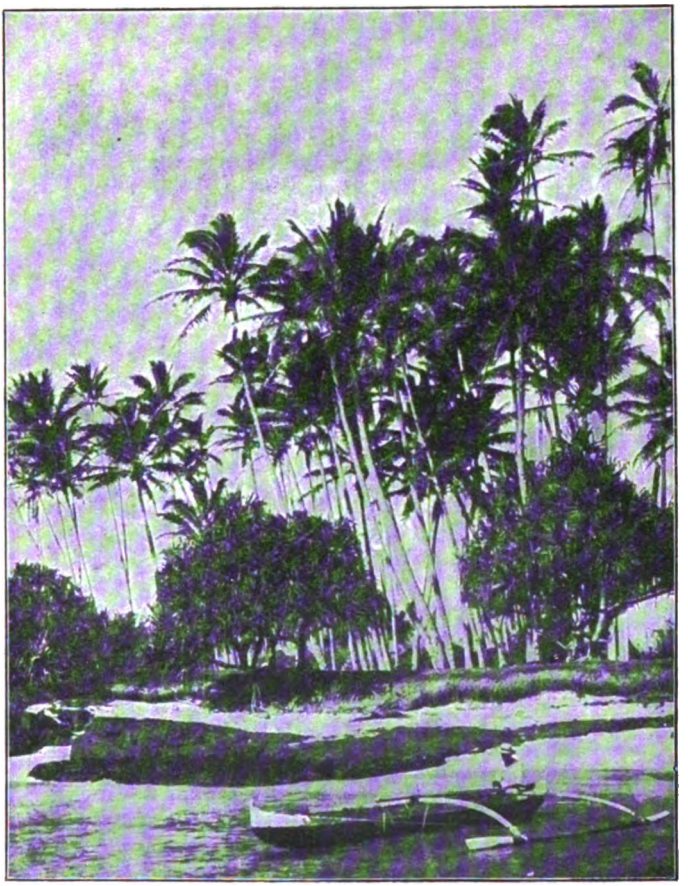


FIG. 822.—Coco-nut Palms at Hilo, Hawaii. *Pandanus odoratissimus* in front of the Palms.

directed, hair-like points, which stand at the level of the constricted portion of the spathe; this is widely open above. These hairs allow insects, attracted by the peculiar scent or seeking warmth, to creep into the lower expanded portion of the spathe, but prevent their return until the female flowers have been pollinated from another individual. When this is accomplished the hairs wither and the anthers open. The escaping insects, now dusted with pollen, may enter other inflorescences and pollinate the flowers.

(*c*) *Flowers zygomorphic*

Order 6. Scitamineae

Tropical plants, sometimes of large size, in a few cases arborescent. Flowers dorsiventral or asymmetrical. Perianth differentiated into

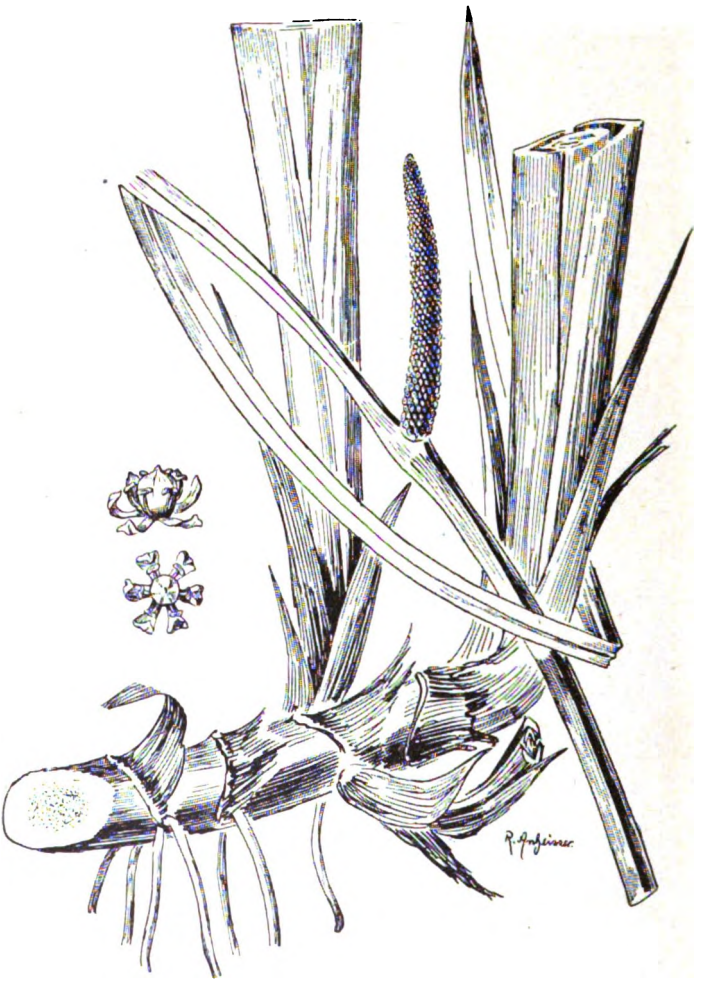


FIG. 823.—*Acorus calamus*. Flowering plant. Single flowers seen from above and from the side. (½ nat. size.)

calyx and corolla. Androecium greatly reduced; some of the stamens represented by staminodes, and resembling the segments of the corolla. Ovary inferior, trilocular. Seeds with perisperm.

Family 1. **Musaceae.**—The Banana (*Musa*) is one of the most important plants

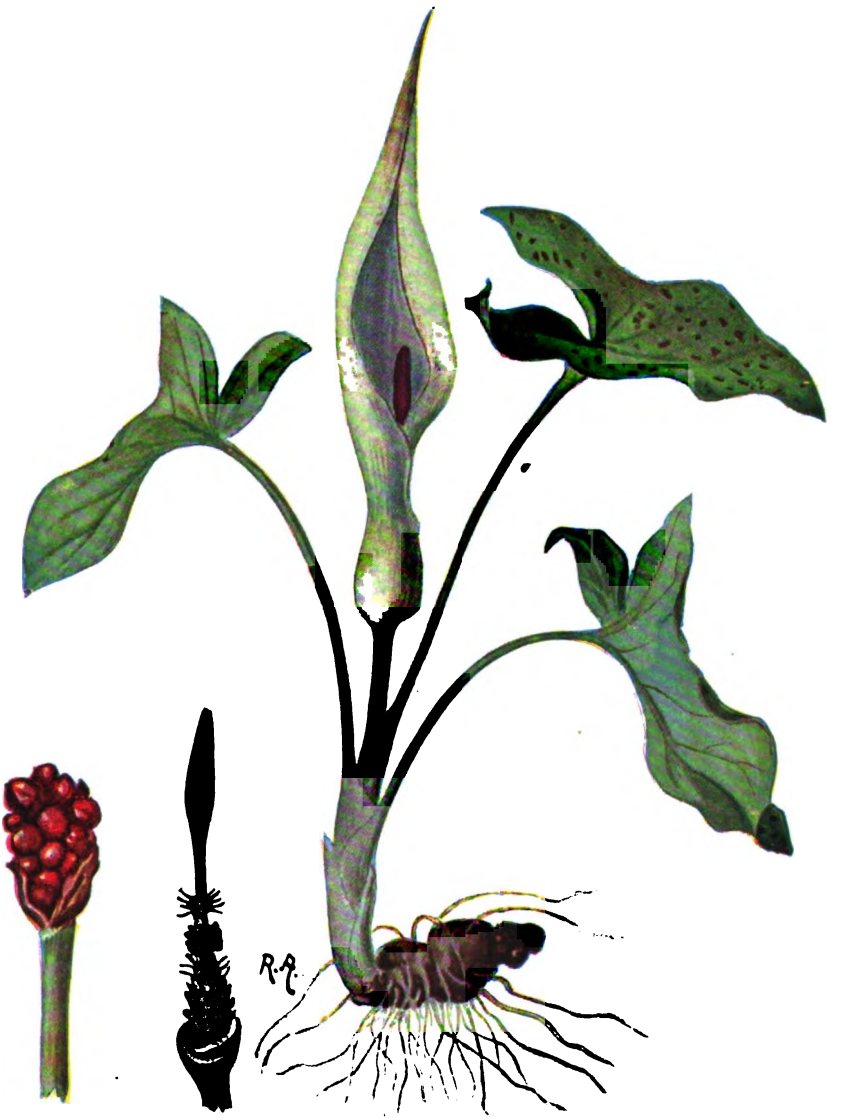


FIG. 824.—*Arum maculatum* (½ nat. size). Inflorescence and fruits (¾ nat. size). *Poisonous.*

of all tropical countries. The apparent, erect stem is formed of the closely overlapping, sheathing bases of the large leaves. Inflorescence, terminal, pendulous,

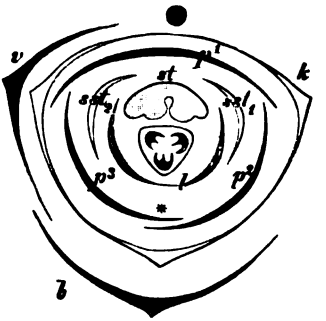


FIG. 825.—Floral diagram of Zingiberaceae (after EICHLER). *b*, Bract; *v*, bracteole; *k*, calyx; p^{1-3}, segments of corolla; sst_1, sst_2, staminodes of the outer whorl of the androecium; * the suppressed stamen of this whorl; *st*, the single fertile stamen; *l*, petaloid staminodes of the inner whorl of the androecium forming what is known as the labellum.

FIG. 826.—*Zingiber officinale.* (¼ nat. size. After BERG and SCHMIDT.) *OFFICIAL.*

bearing the crowded and mainly parthenocarpic (45) berry-like fruits. *M. textilis* yields Manila Hemp. *Ravenala* has a woody stem. *Strelitzia reginae* (Fig. 529) from the Cape is cultivated on account of the beauty of its flowers.

Family 2. **Zingiberaceae.**—Flowers in spikes, which in some cases resemble capitula. Flower dorsiventral. Calyx inconspicuous, tubular. Corolla with three lobes. The outer whorl of the androecium is wanting or represented by two lateral staminodes (Fig. 825, sst_1, sst_2). Only the posterior stamen of the inner whorl (*st*) is fertile; the two others are joined to form the brightly-coloured petaloid labellum (*l*). The style lies in the tubular groove between the thecae of the stamen. Fruit a capsule. Most plants of the family belong to tropical Asia.

Zingiber officinale, the Ginger, is an ancient cultivated plant of Southern Asia, now cultivated throughout the tropics (Fig. 826). The flattened branched rhizome is in contact with the soil by its narrow side. Leaves, two-ranked; main shoot continued by the growth of axillary buds of the lower surface. The leafy shoots, in spite of their length, are composed of the sheaths of the large, simple, entire leaves, the axis remaining extremely short. Only the flowering shoots are solid; they remain shorter and bear scale leaves with large sheaths but no lamina. Bracts large and, especially at their margins, brightly coloured. Flowers, bright yellow, with a conspicuous, violet, and spotted labellum. *Elettaria Cardamomum* and *Curcuma* have the stalks bearing their inflorescences similarly provided with scale leaves. *Alpinia* and *Hedychium*, the latter of which is often cultivated, have on the other hand normal leafy shoots bearing the terminal inflorescence.

OFFICIAL.—*Zingiber officinale*, rhizome yields GINGER. *Elettaria Cardamomum* yields CARDAMOM SEEDS.

Family 3. **Cannaceae.**—Large-leaved herbs; often in cultivation. Flowers asymmetrical (Fig. 827). Only one half stamen fertile (*i.e.* anther with only one theca), the other half being petaloid.

Family 4. **Marantaceae.**—Large-leaved herbs. Leaves with pulvinus at junction of stalk and lamina. Stamen as in preceding order. Arrowroot is obtained from *Maranta arundinacea*.

Order 7. Gynandrae

Family **Orchidaceae.**—Perennial, herbaceous plants growing as epiphytes or in the ground, with hermaphrodite, zygomorphic flowers. Perianth petaloid, the posterior segment of the inner whorl developed as a lip or labellum, which frequently bears a spur. (The "labellum" of the Scitamineae being formed of two staminodes is entirely different morphologically.) Androecium formed of the three anterior stamens only; the middle stamen, belonging to the outer whorl, is fertile; the other two are represented by staminodes. *Cypripedium* has these two lateral stamens of the inner whorl fertile. Gynaeceum formed of three carpels, syncarpous; ovary inferior, unilocular. Fruit, a capsule. Seeds extremely numerous, borne on parietal placentas (Figs. 828, 831). The fertile stamen is adherent to the style and forms with it the COLUMN or GYNOSTEMIUM; this projects more or less in the centre of the flower. The labellum, which serves

as an alighting place for visiting insects, becomes anterior either by the torsion of the whole flower through 180° (cf. Figs. 828, 831) or by the flower being bent backwards.

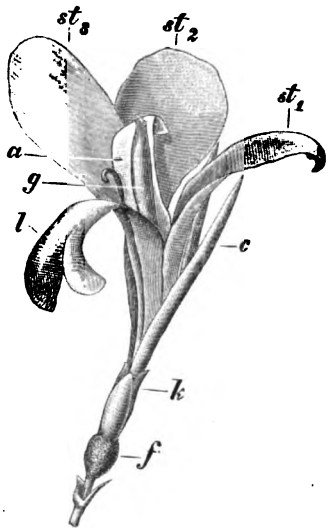


FIG. 827.—Flower of *Canna iridiflora*. *f*, Ovary; *k*, calyx; *c*, corolla; *l*, labellum; st_{1-3}, the other staminodia; *a*, fertile stamen; *g*, style. (½ nat. size.)

The Orchidaceae attain their highest development in the tropics where they form an important part of the epiphytic vegetation. *Orchis*, *Ophrys*, *Gymnadenia*, *Platanthera* with tubers; *Epipactis*, *Cephalanthera*, *Listera* with branched rhizomes; *Neottia*, the Bird's-nest Orchid, *Epipogon*, *Coralliorrhiza*, *Limodorum* almost destitute of chlorophyll. They live saprophytically or more correctly as parasites

FIG. 828.—Orchidaceae. Floral diagram (*Orchis*). (Modified after NOLL.)

at the expense of their mycorrhiza (46). *Cypripedium*, Ladies' Slipper, with two lateral fertile stamens of the inner whorl.

Orchis militaris, which is represented in Fig. 833, will serve as an example for

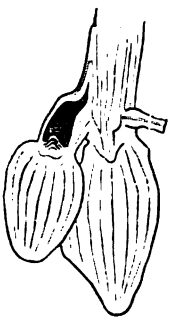


FIG. 829.—*Orchis militaris*. Longitudinal section passing through the old and new tubers. (After LUERSSEN.)

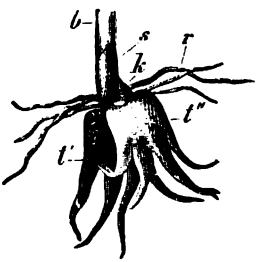


FIG. 830.—Root-system of *Orchis latifolia*. *b*, Base of stem; *s*, scale leaf; *t'*, old, *t''*, young tubers; *k*, bud; *r*, roots. (After H. SCHENCK.)

more detailed consideration. At the period of flowering a pair of fleshy tubers will be found at the base of the plant, both of which are covered with root hairs. The large or brown tuber of more spongy texture continues above into the stem which

terminates in the pyramidal inflorescence; this stem is surrounded at the base by a pair of scale leaves and the sheaths of the 2-4 elongated, elliptical foliage leaves. The smaller tuber is of firmer consistence and of a white colour; it bears, as is shown in the longitudinal section (Fig. 829), a bud on its summit which already shows a pair of scale leaves. This tuber has arisen as an axillary bud in relation to one of the first scale leaves of the plant, and with its tuberous, swollen, first root has broken through the subtending scale leaf (Fig. 829). It is destined to replace the parent plant in the succeeding season.

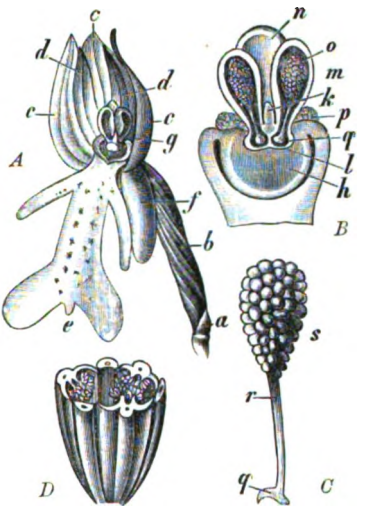


FIG. 831.—*Orchis militaris*. *A*, Flower: *a*, bract; *b*, ovary; *c*, the outer, and *d*, the two anterior inner perigone leaves; *e*, labellum with the spur *f*; *g*, gynostemium. *B*, Flower after removal of all of the perigone leaves with exception of the upper part of the labellum: *h*, stigma; *l*, rostellum; *k*, tooth-like prolongation of the rostellum; *m*, anther; *n*, connective; *o*, pollinium; *q*, viscid disc; *p*, staminodium. *C*, A pollinium: *r*, caudicle; *s*, pollen. *D*, Fruit in transverse section. (After BERG and SCHMIDT.)

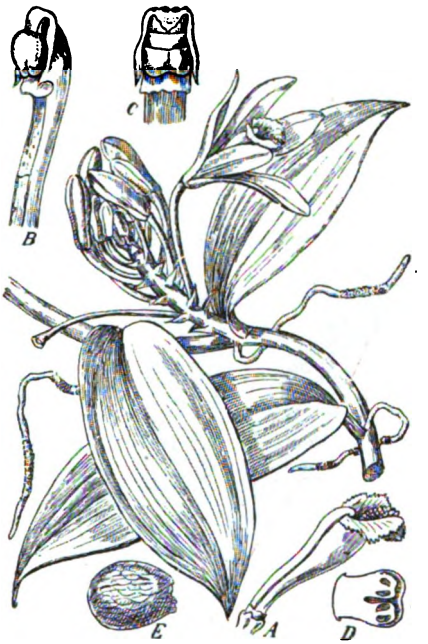


FIG. 832.—*Vanilla planifolia* (reduced. After BERG and SCHMIDT; from ENGLER and PRANTL). *A*, Labellum and gynostemium. *B*, Gynostemium from the side. *C*, Summit of the gynostemium from in front. *D*, Anther. *E*, Seed. (Magnified.)

In considering the flower, the spiral torsion of the ovary, which brings the labellum into the anterior position, must first be recognised. The labellum is tripartite and the larger middle segment is bifid at its free end. At the base of the labellum a spur is formed by the bulging out of this segment of the perianth; this serves as the nectary, and the opening leading into it is situated just below the gynostemium (Fig. 831 *A*, *B*). The latter bears on the side that is turned towards the lower lip, and to an insect alighting on this, the large stigmatic surface (*h*) corresponding to two confluent stigmatic lobes. The third stigmatic lobe is transformed into a structure termed the rostellum (*l*, *k*) and stands in relation to the male organ. The single fertile anther consists of two thecae joined together by the connective which appears as the end of the gynostemium. The whole mass of

Fig. 838.—*Orchis militaris* (½ nat. size).

pollen of each of the two pollen sacs is joined together by an interstitial substance which continues below to form a stalk; the whole structure, which has a waxy consistence, is called a pollinium, and the stalk goes by the name of the caudicle. The caudicles terminate below in contact with the rostellum which forms tough adhesive discs. This relation to the rostellum serves to keep the pollinia, which lie free in the pollen sacs, in position, and the adhesive discs attach the pollinia to any body that comes in contact with them. If an insect alights on the lower lip and attempts to reach the nectar secreted in the spur, its head or tongue must touch the rostellum and the pollinia will become attached to it. As the adhesive discs dry they cause the pollinia to bend forward, so that when the insect visits a second flower they will be brought in contact with the stigmatic surfaces.

All Orchids are similarly adapted to insect visitors, though in many the contrivances are far more complicated; pollination does not take place in the absence of the insects (47). In many cases the adaptations are so specialised to particular insects that no other insect will do instead. Thus *Vanilla* (Fig. 832) brought from its American habitats to other tropical countries remains sterile on account of the absence of the pollinating insect. On this fact being discovered artificial pollination was resorted to and the plants can thus be induced to bear fruits regularly. It should be mentioned that in some forms, *e.g. Vanilla*, the pollen remains powdery. Many tropical

Orchids are cultivated in greenhouses on account of the beauty of their flowers, *e.g. Cattleya, Laelia, Vanda, Dendrobium*, etc.

Fossil Angiosperms [13]

The first undoubted Angiosperms appear in the Upper Cretaceous. They are represented by numerous species which, like the recent forms, can be divided into Monocotyledons and Dicotyledons. The most ancient forms are known only as leaves, so that their determination is a matter of difficulty. They agree essentially with living Angiosperms, and since they show no similarities to Gymnosperms or Pteridophytes, do not aid in bridging over the gap between the Angiosperms and these groups.

The Angiosperms of the Eocene and the Oligocene can be determined with greater certainty; even in Northern Europe representatives of existing tropical and subtropical families occurred, *e.g.* Palmae, *Dracaena*, *Smilax* among Monocotyledons, numerous Querciflorae (esp. *Quercus*), Lauraceae (*Cinnamomum*, etc.), Leguminosae, etc., among Dicotyledons. From the Miocene onwards the specific forms are in part identical with those now living, and in the Quaternary strata all the remains are of existing species. The general character of the Tertiary flora in Europe was, however, very different from that of the present day. It had the aspect of the flora of a much warmer region and (as in the case of the Gymnosperms) contained forms which now exist only in distant regions.

INDEX OF LITERATURE

INTRODUCTION AND MORPHOLOGY BY H. FITTING

Introduction

(1) CHARLES DARWIN, On the Origin of Species by Means of Natural Selection, 1859. (2) E. HAECKEL, Generelle Morphologie der Organismen, 1866, p. 52. (3) C. v. NÄGELI, Theorie der Abstammungslehre, 1884, p. 326; F. A. WENT, Biologisches Zentralblatt, vol. xxvii. 1907, p. 257; K. GOEBEL, Organographie, 2. Aufl. vol. i. 1913, pp. 39 ff.

Section I. Cytology

The Living Cell Contents.—(4) E. STRASBURGER, Progressus rei botanicae, vol. i. 1906, p. 1; E. KÜSTER, Zelle in Handwörterb. der Naturwiss. Jena, vol. x. 1914, p. 748. (5) Literature collected by A. GUILLIERMOND, Revue gén. de Bot. vol. xviii. 1906, p. 392; E. ZACHARIAS, Bot. Ztg. 1907, p. 265; A. MEYER, Die Zelle der Bakterien, Jena, 1912; E. PARAVICINI, Bakt. Zentralbl. II. vol. xlviii. 1918, p. 337. (6) A. J. EWART, Physics and Physiology of Protoplasmic streaming in Plants, Oxford, 1903; PAUL KRETZSCHMAR, Jahrb. f. wiss. Bot. vol. xxxix. 1904, p. 273. (7) J. W. MOLL, Progress. rei botan. vol. ii. 1908, p. 227; E. STRASBURGER, Das kleine bot. Praktikum, 8. Aufl. 1919, and Das botanische Praktikum, 5. Aufl. 1913; H. SIEBEN, Einführung in die bot. Mikrotechnik, Jena, 1913. (8) E. ZACHARIAS, Progress. rei botan. vol. iii. 1910, p. 67. (9) A. FISCHER, Fixierung, Färbung und Bau des Protoplasma, 1899, and A. DEGEN, Bot. Ztg. 1905, 1. Abt. p. 202. (10) N. GAIDUKOV, Dunkelfeldbeleuchtung und Ultramikroskopie in der Biologie und der Medizin, 1910. (11) E. W. SCHMIDT, Progress. rei botan. vol. iv. 1912, p. 163, and Ztschr. f. Botan. vol. iv. 1912, p. 707; J. DUESBERG, References in Ergebn. d. Anatom. u. Entwicklungsgeschichte, vol. xx. 1912, p. 567; K. RUDOLPH, Ber. deutsch. bot. Ges. vol. xxx. 1912, p. 605; G. LEWITZKY, Ber. deutsch. bot. Gesellsch. vol. xxxi. 1913, p. 517; A. SCHERRER, Festschr. z. Einweihung d. Inst. für allg. Bot. Zürich. Jena, 1914; A. GUILLIERMOND, Rev. gén. de bot. vol. xxv. bis, 1914, p. 295; vol. xxvi. 1914, p. 295; FR. MEVES, Arch. f. mikr. Anatomie, vol. lxxxix. 1. Abt. 1917, p. 249; D. M. MOTTIER, Ann. of Bot. vol. xxxii. 1918, p. 91. (12) Cf. the most recent works of GRÉGOIRE and his pupils, and of E. STRASBURGER; also H. LUNDEGÅRDH, Beitr. z. Biol. d. Pflanzen, vol. xi. 1912, p. 373; includes literature. (13) A. GUILLIERMOND, Progr. rei bot. vol. iv. 1913, p. 389; H. v. NEUENSTEIN, Arch. f. Zellforsch. vol. xiii. 1914, p. 1. (14) A. F. W. SCHIMPER, Bot. Ztg. 1880, p. 886, and Jahrb. f. wiss. Bot. vol. xvi. 1885, p. 1; ARTHUR MEYER, Das Chlorophyllkorn, 1883, and Bot. Ztg. 1888, p. 489; J. H. PRIESTLEY and A. A. IRVING, Ann. of Bot. vol. xxi. 1907, p. 407; A. SAPĚHIN, Untersuchungen über die Individualität d.

Plastide, Odessa, 1913; Archiv f. Zellforschung, vol. xiii. 1915, p. 319. ([15]) Especially L. MARCHLEWSKI, E. SCHUNK, N. A. MONTEVERDE, M. TSWETT, R. WILLSTÄTTER; cf. especially R. WILLSTÄTTER and A. STOLL, Untersuchungen über Chlorophyll, Berlin, 1913; C. v. WISSELINGH, Flora, vol. cvii. 1915, p. 371. ([16]) TH. W. ENGELMANN, Bot. Ztg. vol. xl. 1882, p. 663; vol. xli. 1883, p. 1; H. MOLISCH, Bot. Ztg. vol. lxiii. 1905, 1. Abt. p. 131; H. KYLIN, Svensk. bot. tidskr. vol. vi. 1912, p. 531. ([17]) H. KYLIN, Ztschr. f. physiol. Chemie, vol. lxxxii. 1912, p. 221; R. WILLSTÄTTER and H. J. PAGE, Ann. d. Chemie, vol. cccciv. p. 237. ([18]) E. GOERRIG, Beih. Bot. Zentralbl. I. vol. xxxv. 1918, p. 1. ([19]) W. ROTHERT, Bull. intern. ac. sc. de Cracovie sér. B, 1914, p. 1. ([20]) As regards the botanical side the numerous works of E. STRASBURGER, M. TREUB, L. GUIGNARD, W. BELÀJEFF, J. B. FARMER, B. NÊMEC, V. GRÉGOIRE, A. WYGAERTS, E. ESCOYEZ, J. BERGHS, O. ROSENBERG, CH. ALLEN, K. MIYAKE, J. B. OVERTON and others; cf. also TH. BOVERI, Ergebnisse über die Konstitution der chromatischen Substanz des Zellkerns, 1904; M. PICARD, Bull. Torrey Bot. Club, vol. xl. 1913, p. 575. ([21]) G. TISCHLER, Progr. rei bot. vol. v. 1915, p. 164; H. WINKLER, Ztschr. f. Bot. vol. viii. p. 417. ([22]) E. STRASBURGER in Wiesner-Festschrift, 1908, p. 24. ([23]) R. A. HARPER, Jahrb. f. wiss. Bot. vol. xxx. 1897, p. 249; P. N. SCHÜRHOFF, Jahrb. f. wiss. Bot. vol. lvii. 1917, p. 363.

The Larger Non-living Inclusions of the Protoplasts. ([24]) H. MOLISCH, Mikrochemie der Pflanze, Jena, 1913; O. TUNMANN, Pflanzenmikrochemie, Berlin, 1913. ([25]) J. DEKKER, Die Gerbstoffe, Berlin, 1913. ([26]) R. WILLSTÄTTER, Sitzungsber. preuss. Akad. d. Wiss. 1914, pp. 402, 769; H. SCHRODER, Ztschr. f. Bot. vol. ix. 1917, p. 546; cf. also H. MOLISCH, Bot. Ztg. 1905, 1. Abt. p. 161; also B. L. BUSCALIONI and G. POLLACCI, Atti istit. bot. Univ. Pavia, N.S. vol. viii. 1903, pp. 135 ff.; O. GERTZ, Studier öfver Anthocyan, Lund, 1906. ([27]) A. TSCHIRCH, Die Harze und die Harzbehälter, 1900. ([28]) Literature in A. GUILLIERMOND and J. BEAUVERIE, Ann. des sc. nat. Bot. IX. Sér. vol. viii. 1908, p. 173. ([29]) C. NÄGELI, Die Stärkekörner, 1858; A. F. W. SCHIMPER, Bot. Ztg. 1881, p. 223; A. MEYER, Unters. über die Stärkekörner, 1895; H. PRINGSHEIM, Landwirtsch. Versuchsstationen, vol. lxxxiv. 1914, p. 267.

The Cell-Wall.—([30]) Literature to 1904 in L. GAUCHER, Étude générale sur la membrane cellulaire chez les végétaux, 1904, and since in FR. CZAPEK, Biochemie der Pflanze, 2. Aufl. vol. i. 1913, p. 629; O. RICHTER, Ztschr. f. wiss. Mikr. vol. xxii. 1905, p. 194; Zur Membranstreifung W. KRIEG, Beih. z. bot. Zentralbl. vol. xxi. 1907, p. 245. ([31]) E. HANNIG, Flora, vol. cii. 1911, p. 209. ([32]) F. CZAPEK, Biochemie der Pflanzen, 2. Aufl. vol. i. 1913, p. 629; PETER KLASON, Schriften des Vereins der Zellstoff- und Papier-Chemiker, vol. ii. 1911; FR. CZAPEK, Ztschr. f. Bot. vol. iii. 1911, p. 500; J. KÖNIG and E. RUMP, Chemie und Struktur der Pflanzen-Zellmembran, Berlin, 1914; C. G. SCHWALBE, Die Chemie der Zellulose, 2. Aufl. Berlin, 1918. ([33]) Cf. F. CZAPEK in ([30]), vol. i. p. 634 ff.; A. VIEHOEVER, Ber. deutsch. bot. Gesellsch. vol. xxx. 1912, p. 443. ([34]) F. EHRLICH, Chemiker-Zeitg. vol. xli. 1917, p. 197. ([35]) VAN WISSELINGH, Archives néerland. vol. xxvi. 1892, p. 305, and vol. xxviii. 1898, p. 373. ([36]) ORMOND BUTLER, Ann. of Bot. vol. xxv. 1911, p. 107; gives the literature on p. 150; J. GRÜSS, Jahrb. f. wiss. Bot. vol. xlvii. 1910, p. 391.

Section II. Histology

([37]) A. DE BARY, Vergl. Anat. d. Vegetationsorgane, 1877; G. HABERLANDT, Physiologische Pflanzenanat. 5. Aufl. 1918; H. SOLEREDER, Syst. Anat. d.

Dikotyledonen, 1899; English translations of the three preceding works; W. ROTHERT, Gewebe. Handwörterb. d. Naturwiss. iv. Jena, 1913, p. 1144; E. STRASBURGER, cited in (7); A. MEYER, Erstes mikroskop. Praktikum, 3. Aufl. Jena, 1915. (38) For the literature cf. in (4) (39) G. KRABBE, Das gleitende Wachstum b. d. Gewebebildung der Gefässpflanzen, Berlin, 1886; F. NEEF, Ztschr. f. Bot. vol. vi. 1914, p. 465. (40) L. DIELS, Flora, vols. cxi.-cxii. 1918, p. 490. (41) On Stomata E. STRASBURGER, Jahrb. f. wiss. Bot. vol. v. 1866, p. 297; S. SCHWENDENER, Monatsber. d. Berl. Akad. d. Wiss. 1881, p. 883, etc.; S. H. ECKERSON, Bot. Gaz. vol. xlvi. 1908, p. 221. (42) G. HABERLANDT, Die Sinnesorgane im Pflanzenreich, 2. Aufl. 1906. (43) G. MYLIUS, Biblioth. botan., Heft 79, 1912. (44) S. SCHWENDENER, Das mechanische Prinzip im Bau der Monokotylen, 1874; H. AMBRONN, Jahrb. f. wiss. Bot. vol. xii. 1879. (45) A. W. HILL, Ann. of Bot. vol. xv. 1901, p. 575, and vol. xxii. 1908, p. 245; A. F. HEMENWAY, Botan. Gazette, vol. lv. 1913, p. 236; E. W. SCHMIDT, Bau u. Funktion der Siebröhre, etc. Jena, 1917. (46) W. ROTHERT, Abhandlungen d. Akad. d. Wiss. Krakau, 1899, p. 433. (47) H. MOLISCH, Studien über Milchsaft und Schleimsaft der Pflanzen, 1901. (48) M. NIEUWENHUIS–v. UEXKÜLL–GÜLDENBAND, Rec. trav. bot. néerland. vol. xi. 1914, p. 291.

Section III. Organography

Structure of the Thallus and of the Typical Cormus.—(49) K. GOEBEL, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, 1883, and Organographie der Pflanzen, 1898–1901, 2. Aufl. vol. i. 1913, vol. ii. 1915–18; J. VELENOVSKY, Vergleichende Morphologie der Pflanzen, 4 vols. Prag, 1905–14; KERNER VON MARILAUN-HANSEN, Pflanzenleben, 3. Aufl. vol. ii. 1913 (English translation); F. PAX, Allgemeine Morphologie der Pflanzen, 1890. (50) F. OLTMANNS, Morphologie und Biologie der Algen, 1904; A. DE BARY, Vergl. Morphol. u. Biologie der Pilze, 1884 (English translation). (51) F. SCHÜTT, Das Pflanzenleben d. Hochsee, 1893. (52) E. DE WILDEMAN, Mém. couronnés et publiés par l'Acad. des sciences de Belgique, vol. liii. 1893. (53) H. LEITGEB, Untersuchungen über die Lebermoose, vols. i.-vi. 1874–79; K. GOEBEL, Organographie, 2. Aufl. vol. ii. Jena, 1915; D. H. CAMPBELL, The Structure and Development of Mosses and Ferns, 2nd ed. 1905. (54) Cf. GOEBEL, cited in (53). (55) F. HERRIG, Flora, vol. cvii. 1914, p. 327. (56) W. HOFMEISTER, Allgemeine Morphologie der Gewächse, Leipzig, 1868. (57) S. SCHWENDENER, Mechanische Theorie der Blattstellungen, 1878, and many papers in the Sitzungsber. d. Akad. d. Wiss. Berlin; HANS WINKLER, Jahrb. f. wiss. Bot. vol. xxxvi. 1901, p. 1, and vol. xxxviii. 1903, p. 501; other literature in these. (58) See the works quoted under (37). (59) E. STRASBURGER, Über den Bau und die Verrichtung der Leitungsbahnen in den Pflanzen, 1891, pp. 98, 297; G. CHAUVEAUD, Ann. d. scienc. nat. bot. IX. Sér. vol. xiii. 1911, p. 113; F. J. MEYER, Progress. rei bot. vol. v. 1917, p. 521. (60) J. C. SCHOUTE, Die Stelärtheorie, 1902; H. SOLMS-LAUBACH, Bot. Ztg. 1903, 2. Abt. Sp. 37, 147; A. G. TANSLEY, New Phytologist, No. 2, 1908; F. J. MEYER, Beihefte z. bot. Zentralbl. vol. xxxiii. 1. Abt. 1917, p. 129. (61) v. DEINEGA, Flora, vol. lxxxv. 1898, p. 439. (62) M. NORDHAUSEN, Ber. deutsch. bot. Gesellsch. vol. xxx. 1912, p. 483. (63) E. NEUMANN-REICHARDT, Beitr. z. allg. Bot. vol. i. 1917, Heft 3. (64) K. DOMIN, Ann. d. jard. bot. Buitenzorg, vol. xxiv. 1911, p. 117. (65) E. BRICK, Beih. z. bot. Zentralbl. vol. xxxi. I. 1913, p. 209; P. NEESE, Flora, vol. cix. 1917, p. 144. (66) M. RACIBORSKI, Handwörterb. d. Naturwiss. vol. ix. 1913, Jena, p. 352. (67) K.

GOEBEL, Einleitung in die experimentelle Morphologie d. Pflanzen, 1908, p. 165. ([68]) E. RÜTER, Flora, vol. cx. 1918, p. 195. ([69]) F. SCHWARZ, Unters. a. d. bot. Inst. in Tübingen, vol. i. 1883, p. 135. ([70]) K. KROEMER, Biblioth. botan., Heft 59, 103; H. MÜLLER, Bot. Ztg. vol. lxiv. 1906, p. 53; M. PLAUT, Die physiol. Scheiden d. Gymnospermen, Equisetaceen u. Bryophyten, Diss. Marburg, 1909; Mitteil. d. Kais.-Wilh. Inst. f. Landw. Bromberg, 1910, vol. iii. p. 63; Jahrb. f. wiss. Bot. vol. xxviii. 1910, p. 143. ([71]) G. RUMPF, Bibl. botan. Heft 42, 1904. ([72]) PH. VAN TIEGHEM, Traité de botan. 2nd ed. 1891, p. 700; includes the literature. ([73]) FR. WETTSTEIN, Beihefte z. bot. Zentralbl. II. vol. xx. 1906, p. 1. ([74]) GOEBEL, quoted in ([67]). ([75]) M. BÜSGEN, Bau u. Leben unserer Waldbäume, 2. Aufl. Jena, 1917; H. LUNDEGÅRDH, Kungl. Svensk. Vet. Akad. Handl. vol. lvi. 1916, No. 3. ([76]) J. C. SCHOUTE, Ann. jard. bot. Buitenzorg, 2e sér. vol. xi. 1912, p. 1; A. BORZI and G. CATALANO, Reale acad. d. Lincei, vol. cccix. 1912, p. 167. ([77]) Cf. the works under ([49]) and STRASBURGER under ([59]). ([78]) J. KLINKEN, Bibl. botanica, Heft 84, 1914. ([79]) E. ANTEVS, Progr. rei bot. vol. v. 1917, p. 285. ([80]) O. GERTZ, Lund's univers. årsskrift N.F. II. vol. xii. 1916. ([81]) H. JANSSONIUS, De tangentiale groei van eenige pharm. Basten. Diss. Groningen, 1918. ([82]) P. BÄSICKE, Bot. Ztg. 1908, p. 55. ([83]) E. KÜSTER, Pathologische Pflanzenanatomie, 2. Aufl. 1916.

Adaptations of the Cormus to its Mode of Life and to the Environment.—([84]) K. GOEBEL, Pflanzenbiologische Schilderungen, Marburg, 1889–93; F. A. W. SCHIMPER, Pflanzengeographie auf physiol. Grundlage, Jena, 1898 (English translation, 1903); FR. W. NEGER, Biologie d. Pflanzen, Stuttgart, 1913; G. KARSTEN, Lehrbuch d. Biologie, 2. Aufl. Leipzig, 1914; E. WARMING–P. GRAEBNER, Lehrb. d. ökolog. Pflanzengeographie, 3. Aufl. Berlin, 1918 (English translation), and the works named under ([49]). ([85]) H. SCHENCK, Biologie der Wassergewächse, Bonn, 1886; K. GOEBEL, Pflanzenbiolog. Schilderungen, 1891, vol. ii. p. 215; H. GLÜCK, Untersuchungen über Wassergewächse, 3, Jena, 1905–1911. ([86]) J. SHREVE, Journ. of Ecology, vol. ii. 1914, p. 82. ([87]) K. GOEBEL, cf. ([84]); O. RENNER, Flora, vol. c. 1910, p. 451; MARLOTH, Flora des Kaplandes; H. FITTING, Ztschr. f. Bot. vol. iii. 1911, p. 109; A. ENGLER, Sitzungsber. d. kgl. preuss. Akad. d. Wiss. 1914, p. 564; in addition numerous works on the Xerophytes of American deserts in the Publicat. of the Carnegie Institution, Washington. ([88]) E. WARMING, Mém. acad. royal. d. scienc. de Danemark, 8e sér. vol. ii. 1918, p. 297. ([89]) H. SCHENCK, Beitr. z. Biologie und Anatomie d. Lianen, Jena, 1892–93. ([90]) K. GOEBEL, Pflanzenbiologische Schilderungen, vol. i. p. 147; A. F. W. SCHIMPER, Die epiphytische Vegetation Amerikas, Jena, 1888. ([91]) CH. DARWIN, Insectivorous Plants, 1876; K. GOEBEL, Pflanzenbiologische Schilderungen, 1893, vol. ii.; CLAUTRIAU, Mém. publ. par l'acad. de Belgique, vol. lix. 1900; G. SCHMID, Flora, vol. iv. 1912, p. 335. ([92]) L. KOCH, Die Klee- und Flachsseide, Heidelberg, 1880; PEIRCE, Annals of Botany, 8, 1894; KOCH, Entwicklungsgesch. d. Orobanchen, Heidelberg, 1887; H. SOLMS-LAUBACH, Rafflesiaceen in ENGLER, Das Pflanzenreich, Leipzig, 1901.

Organs of Reproduction.—([93]) The works named under ([49, 50, 53]). ([94]) W. N. STEIL, Bot. Gazette, vol. lix. 1915, p. 254. ([95]) H. WINKLER, Progr. rei botan. vol. ii. 1908, p. 293; A. ERNST, Zeitschr. f. indukt. Abstammungslehre, vol. xvii. 1917, p. 203; A. ERNST, Bastardierung als Ursache der Apogamie im Pflanzenreiche, Jena, 1918. ([96]) H. KYLIN, Ztschr. f. Bot. vol. viii. 1916, p. 545; O. RENNER, Biolog. Zentralbl. vol. xxxvi. 1916, p. 337; J. BUDER, Ber. d. deutsch. bot. Gesellsch. vol. xxxiv. 1916, p. 559. ([97]) CH. J. CHAMBERLAIN and J. M. COULTER, Morphology of Gymnosperms, 1910, and Morphology of Angiosperms, 1903.

(98) W. EICHLER, Blütendiagramme, 1875–78. (99) H. MÜLLER, Die Befruchtung der Blumen d. Insekten, Leipzig, 1873, and Alpenblumen, 1881; O. KIRCHNER, Blumen und Insekten, 1911. (100) A. KERNER VON MARILAUN, Pflanzenleben, 2. Aufl. vol. ii. 1905 (English translation). (101) G. KLEBS, Untersuch. aus dem botan. Institut Tübingen, vol. i. 1885. (102) E. STRASBURGER in papers published in vols. xlii. xliv. and xlv. of the Jahrb. f. wiss. Bot. 1906–1908 and in Histol. Beitr. Heft 7, 1909. (103) J. B. FARMER, Quart. Journ. Micr. Soc. vol. xlviii. 1905, p. 489; D. M. MOTTIER, Ann. of Bot. vol. xxi. 1907, p. 309; V. GRÉGOIRE, La Cellule, vol. xxii. 1905, p. 221 ff. and vol. xxvi. 1910, p. 223; includes the literature to 1910; PICARD, cf. (20).

Section IV. The Theory of Descent and the Origin of New Species

(104) CH. DARWIN, On the Origin of Species by Means of Natural Selection, 1859; *ibid.* Animals and Plants under Domestication; *ibid.* The Descent of Man; E. HAECKEL, Generelle Morphologie, Neudruck, Berlin, 1906; Natürliche Schöpfungsgeschichte; A. WEISMANN, Vorträge über die Deszendenztheorie, 3. Aufl. Jena, 1913; J. P. LOTSY, Vorlesungen über Deszendenztheorien, Jena, 1906; L. PLATE, Der gegenwärtige Stand der Abstammungslehre, Leipzig, 1909; ABEL, BRAUER, etc., Abstammungslehre, 12 Vorträge, Jena, 1911; K. C. SCHNEIDER, Einführung in die Deszendenztheorie, 2. Aufl. Jena, 1911; R. HESSE, Abstammungslehre und Darwinismus (Aus Natur und Geisteswelt, vol. xxxix.), 5. Aufl. 1918; L. PLATE, Deszendenztheorie, Handwörterb. d. Naturwiss. vol. ii. Jena, 1912, p. 897 ff. (105) J. LAMARCK, Philosophie zoologique, 1809; H. SPENCER, The Principles of Biology, 1876; C. v. NÄGELI, Mechanisch-physiologische Theorie der Abstammungslehre, München, 1884; R. SEMON, Die Mneme, 3. Aufl. 1911; A. PAULY, Darwinismus und Lamarckismus, München, 1905; R. v. WETTSTEIN, Der Neo-Lamarckismus, Jena, 1903; Handb. d. system. Botanik, Leipzig and Wien, 2. Aufl. 1911, p. 32; O. HERTWIG, Das Werden der Organismen, 2. Aufl. Jena, 1918; C. DETTO, Die Theorie der direkten Anpassung, Jena, 1904. (106) G. ROMANES, Darwin and after Darwin; L. PLATE, Selektionsprinzip und Probleme der Artbildung, 3. Aufl. Leipzig, 1908; A. WEISMANN, Die Selektionstheorie, Jena, 1909; C. DETTO, Die Theorie der direkten Anpassung, Jena, 1904.

PHYSIOLOGY BY L. JOST

Introduction

(1) The fullest exposition of plant-physiology is to be found in PFEFFER, Physiology of Plants (Eng. trans. 1900–1906). This deals with the literature from 1897 to 1904, and only the fundamental work and the most important recent literature is given below. As an introductory work on the subject may be mentioned JOST, Vorlesungen über Pflanzenphysiologie, 3. Aufl. Jena, 1913 (English translation). As introductory to experimental work DETMER (1912), Das kleine pflanzenphysiologische Praktikum, 4. Aufl. Jena; CLAUSSEN (1910), Pflanzenphys. Versuche und Demonstrationen für die Schule, 2. Aufl. Leipzig and Berlin. (2) BERNARD (1878), Leçons sur les phénomènes de la vie, Paris; SACHS (1882), Vorlesungen über Pflanzenphysiologie, Leipzig, Vorlesung 12; KLEBS (1904), Biol. Cbl. 24, distinguishes three sorts of causes: (1) external; (2) internal; (3) the specific structure. Under the last he includes the determinants (p. 296) which are the causes of specific structure. As internal causes he recognises all within the plant that acts on these determinants. (3) MOLISCH (1897), Das Erfrieren der Pflanzen, Jena; MEZ (1905), Flora, 94; WINKLER (1913), Jahrb. f. wiss. Bot. 52; MAXIMOW

(1914), *ibid.* 53; KYLIN (1917), Ber. bot. Ges. 35. The significance of temperature for the geographical distribution of plants is more fully treated in SCHIMPER (1898), Pflanzengeographie, Jena (English translation); SOLMS-LAUBACH (1905), Gesichtspunkte der Pflanzengeographie, Leipzig; IHNES's Phaenological Chart of the Coming of Spring in Europe should be mentioned (Petermanns Mitt. 1905, Heft 5). (4) SCHIMPER, see (3). (5) BECQUEREL (1909 and 1910), Compt. rend. Paris, 148 and 150; NEUBERGER (1914), Botan. Centralblatt, 126, p. 665 (Ref.); ESTREICHER-KIERSNOWSKA, *ibid.* 134, p. 244 (Ref.).

Metabolism

(6) CZAPEK (1905), Biochemie der Pflanzen, Jena, vol. i. [2. Aufl. 1913]; EULER (1908), Grundlagen und Ergebnisse der Pflanzenchemie, Braunschweig; NATHANSON (1910), Stoffwechsel der Pflanzen, Leipzig.

Chemical Composition; Absorption.—(7) E. WOLF (1871, 1880), Aschenanalysen von land- und forstwirtschaftlichen Produkten, Berlin; KÖNIG (1882), Zusammensetzung der menschlichen Nahrungs- und Genussmittel, Berlin. (8) NÄGELI (1858), Pflanzenphys. Unters. 3; OSTWALD (1909), Grundriss der Kolloidchemie, Lpzg. (9) PFEFFER (1877), Osmotische Untersuchungen, Leipzig; *ibid.* (1886), Unters. a.d. bot. Institut Tübingen, 2; *ibid.* (1890), Abh. d. math.-phys. Kl. d. sächs. Gesellsch. Leipzig; DE VRIES (1884), Jahrb. wiss. Botanik, 14. (9a) RIPPEL (1918), Ber. bot. Ges. 36; HANSTEEN-CRANER (1914), Jahrb. wiss. Bot. 53. (10) URSPRUNG and BLUM (1916), Ber. bot. Gesellsch. 34; BLUM (1916), Beihefte bot. Centralbl. (I.) 33. (11) ESCHENHAGEN (1889), Diss. Leipzig; LEPESCHKIN (1910), Berichte d. bot. Ges. 28; TRÖNDLE (1910), Jahrb. wiss. Botanik, 48; FITTING (1915), Jahrb. wiss. Bot. 56. (12) FITTING (1911), Ztschr. f. Bot. 3; BRIGGS and SHANTZ (1913), Flora, 105; SHIVE and LIVINGSTON (1914), Plant World, 17. (13) BURGERSTEIN (1904), Transpiration der Pflanzen, Jena; RENNER (1910), Flora, 100; *ibid.* (1912), Ber. bot. Ges. 30. (14) HÖHNEL (1879, 1880), Mitt. a. d. forstl. Versuchswesen Österreichs, 2; BRIGGS and SHANTZ (1914 and 1916), Journ. of Agric. Research, 3 and 5. (15) STAHL (1894), Bot. Ztg. 52; STEIN (1912), Ber. bot. Ges. 30; MOLISCH (1912), Ztschr. f. Bot. 4; NEGER (1912), Ber. bot. Ges. 30; WEBER, Fr. (1916), Ber. bot. Ges. 34; WEBER (1916), Ber. bot. Ges. 34. (16) BÜRGERSTEIN, see (13); LEPESCHKIN (1906), Beihefte bot. Centralbl. 19; BRÜCKE (1844), Annalen d. Physik, 63; (OSTWALDS Klassiker, No. 95); PFEFFER (1877), Osmotische Untersuchungen, Leipzig; *ibid.* (1890), Abh. d. Kgl. Gesellsch. d. Wiss. Leipzig; WIELER (1893), Cohns Beitr. z. Biologie, 6; RUHLAND (1915), Jahrb. wiss. Bot. 53; FABER, v. (1915), Jahrb. wiss. Bot. 56. (17) LEPESCHKIN and PFEFFER, see (16). (18) STRASBURGER (1891), Bau u. Verrichtungen d. Leitungsbahnen, Jena; URSPRUNG (1907), Biolog. Centralbl. 27; Jahrb. wiss. Bot. 44; RENNER (1913), Handw. d. Naturw. 10; EWART (1908), Philos. Transact. Roy. Soc. (B) 199; *ibid.* (1910), Annals of Botany, 24. (19) DIXON (1909), Prog. rei bot. 3; DIXON and JOLY (1894), Annals of Bot. 8; ASKENASY (1895, 1896), Verh. naturw. Verein Heidelberg, N.F. 5; STEINBRINCK (1906), Jahrb. wiss. Bot. 42; RENNER (1911), Flora, 103; (1915) Jahrb. wiss. Bot. 56; (1918) Ber. bot. Ges. 36; HOLLE (1915), Flora, 108; JOST (1916), Z. f. Bot. 8; URSPRUNG (1915, 1916), Ber. bot. Ges. 33 and 34; LINDNER (1916), Beitr. z. Biologie, 13; NORDHAUSEN (1917), Jahrb. wiss. Bot. 58. (19a) KNOP (1861), Landw. Versuchsstationen, 3; APPEL (1918), Zeitschr. f. Bot. 10. (20) RICHTER (1919), Sitzungsber. Wien. Akad. 118, 2. Abt.; *ibid.* (1911) Die Ernährung der Algen, Leipzig; OSTERHOUT (1912), Bot. Gaz. 54.—The behaviour of halophytes in relation to sodium chloride is not made perfectly clear by the work of PEKLO (Öst.

botan. Zeitschr. 1912). ([21]) KRATZMANN (1913), Sitzungsber. Wien. Akad. 1. Abt. ([22]) HÖBER (1911), Physikal. Chemie der Zelle, 3. Aufl. Leipzig; RUHLAND (1908), Jahrb. wiss. Botanik, 46; (1915) *ibid.* 55; MEURER (1909), *ibid.*; CZAPEK (1911), Methode zur direkten Bestimmung der Oberflächenspannung der Plasmahaut, Jena; (1915) Jahrb. wiss. Bot. 56; PANTANELLI (1915), *ibid.* 56; OSTERHOUT (1915, 1916), Botan. Gazette, 59, 61; FITTING (1915, 1917), Jahrb. wiss. Bot. 56, 57; HÖFFLER (1918), Ber. bot. Ges. 36. ([23]) PFEFFER (1886), Unters. botan. Institut Tübingen, 2; RUHLAND (1914), Jahrb. wiss. Bot. 54; KÜSTER (1911), Jahrb. wiss. Bot. 50; WISSELINGH (1913), Proc. Ak. v. Wetensch. 15. ([24]) KUNZE (1906), Jahrb. wiss. Bot. 42; BACHMANN, Ber. bot. Ges. 22 and 29; SCHULOW (1913), Ber. bot. Ges. 31. ([25]) BROWN and ESCOMBE (1900), Philos. Transact. (B) 193. ([26]) MAYER, ADOLF (1901), Agrikulturchemie, 5. Aufl. Heidelberg. ([27]) SCHIMPER (1889), Pflanzengeographie auf biolog. Grundlage, Jena (English Translation); ENGLER (1879–82), Vers. einer Entwicklungsgeschichte d. Pflanzenwelt, Lpzg.; SOLMS-LAUBACH (1905), Die leitenden Gesichtspunkte d. Pflanzengeographie, L. ([28]) CLAUSSEN (1901), Flora, 88; LINDNER (1916), Beitr. z. Biologie, 13.

Assimilation and Translocation.—([28a]) WILLSTÄTTER and STOLL (1918), Unters. üb. Assimilation der Kohlensäure; WISLICENUS (1918), Ber. chem. Ges. 51; SCHRÖDER, H. (1917), Die Hypothesen über die chem. Vorgänge b. d. Kohlensäureassimilation (1918), Ber. d. bot. Ges. 36. ([29]) REINKE (1884), Bot. Ztg. 42; ENGELMANN (1884), Bot. Ztg. 42; TIMIRIAZEFF (1903), Proc. R. Soc. (B) 72; KNIEP and MINDER (1909), Zeitschr. für Botanik, 3; RICHTER (1912), Ber. bot. Ges. 30; URSPRUNG (1918), Ber. bot. Ges. 36. ([29a]) BROWN (1905), Proc. R. Soc. (B) 76; PURIEWITSCH (1914), Jahrb. wiss. Bot. 53. ([30]) WILLSTÄTTER and STOLL (1915), Sitzungsber. Berl. Akad.; WILLSTÄTTER in ([28a]). ([30a]) SCHRÖDER (1919), Die Naturwissenschaften. ([31]) NATHANSOHN (1910), Stoffwechsel der Pflanzen, Leipzig; ANGELSTEIN (1910), Beitr. zur Biologie, 10; KNIEP (1915), Jahrb. wiss. Bot. 56. ([32]) HANSEN (1912), Nat. Rundschau, 27; FISCHER (1912), Ber. bot. Ges. 30. ([32a]) A. MEYER (1918), Ber. bot. Ges. 36. ([33]) KREUSLER, Landw. Jahrb. 14, 16, 17, 19; GILTAY (1898), Annales jard. bot. de Buitenzorg, 15; SACHS (1884), Arbeiten Bot. Institut Würzburg, 3; BROWN and ESCOMBE (1900), Philos. Transactions R. Soc. (B) 193; BLACKMAN (1905), Annals of Botany, 19; *ibid.* Proceedings Royal Soc. (B) 76; THODAY (1910), Proc. Royal Soc. (B) 82. ([34]) WINOGRADSKI (1890–91), Annales Institut Pasteur, 4 and 5; HUEPPE (1906), Ergebnisse d. intern. bot. Congr. Wien; KRZEMIENIEWSKI (1908), Bull. acad. Cracovie; NIKLEWSKI (1910), Jahrb. wiss. Bot. 48; LEBEDEFF (1909), Ber. deutsch. bot. Ges. 27; LIESKE (1911), Jahrb. wiss. Bot. 49; KEIL (1912), Beitr. z. Biologie, 11; MÜNZ (1915), Z. Phys. d. Methanbakterien, Diss. Halle. ([35]) DARWIN (1876), Insectivorous Plants; GOEBEL (1893), Pflanzenbiolog. Schilderungen, 2, Marburg; CLAUTRIAU (1900), Mém. publ. p. l'acad. de Belgique, 59; SCHMID (1912), Flora, 104; LÜTZELBURG (1910), Flora, 100; RUSCHMANN (1914), Z. Ökologie von Pinguicula . . ., Diss. Jena; STERN (1917), Flora, 109. ([36]) HEINRICHER, Jahrb. wiss. Bot. 31, 32, 36, 37, 46, 47. ([37]) WINOGRADSKI (1895), Archives d. sc. biologiques, 3; *ibid.* (1902), Centralblatt f. Bakteriologie (II.), 9]; KOCH (1904) in LAFAR, Technische Mykologie, 3, Jena; HELLRIEGEL and WILFARTH, Stickstoffnahrung d. Gramineen u. Leguminosen, Berlin; HILTNER (1904) in LAFAR, Technische Mykologie, 3, Jena; DE BARY (1879), Erscheinung d. Symbiose, Strassburg; FISCHER, A. (1903), Vorlesungen über Bakterien, 2. Aufl. Jena; BREDEMANN (1909), Centralbl. Bakt. 2. Abt. 23; KRZEMIENIEWSKI (1908), Bull. acad. Cracovie; STOKLASA (1908), Centralbl. Bakt. (2. Abt.) 21. ([38]) LAWES,

GILBERT and PUGH (1862), Philos. Transact. 151; SCHULTZ-LUPITZ (1881), Landw. Jahrb. 10. ([39]) KAMIENSKI (1881), Botan. Ztg. 39; FRANK (1887, 1888), Berichte bot. Gesellsch. 5, 6; STAHL (1900), Jahrb. wiss. Bot. 34; SHIBATA (1902), Jahrb. wiss. Bot. 37; BERNARD (1909), Annales des sciences nat. (9) 9; BURGEFF (1909), Wurzelpilze der Orchideen, Jena; WEYLAND (1912), Jahrb. wiss. Bot. 51; MIEHE (1918), Flora, 111. ([39a]) NIENBURG (1917), Ztschr. f. Bot. 9. ([40]) v. FABER (1912), Jahrb. wiss. Bot. 51; (1914) *ibid.* 54; MIEHE (1913 and 1917), *ibid.* 55 and 58. ([40a]) The remarkable discoveries of BIEDERMANN, 1916 (Fermentforschung) on the origin of diastase in boiled "starch solution" are still too isolated to be treated in the text. ([41]) GREEN (1901), The Soluble Ferments and Fermentation; DUCLAUX (1899), Traité de microbiologie, **2**, Paris; BREDIG (1891), Anorgan. Fermente, Leipzig; HÖBER (1911), Physikal. Chemie d. Zelle, 3. Aufl. Leipzig; OPPENHEIMER (1910), Die Fermente, 3. Aufl. L. ([42]) CZAPEK (1897), Sitzungsberichte Wiener Akad. 106; DELEANO (1911), Jahrb. wiss. Bot. 49. ([43]) TEODORESCO and POPESCO, Annal. sc. de l'univ. de Jassy, 9; SWART (1914), Stoffwanderung in ablebenden Blättern, Jena. ([44]) CZAPEK and EULER in ([5]).

Respiration and Fermentation.—([45]) WORTMANN (1880), Arb. bot. Institut Würzburg, 2; PFEFFER (1885), Unters. bot. Inst. Tübingen, 1; JOHANNSEN (1885), Unters. a. d. bot. Inst. Tübingen, 1; STICH (1891), Flora, 74; KOSTYTSCHEW (1913), Ber. bot. Ges. 31. ([46]) PALLADIN (1909), Biochem. Zeitschr. 18; BACH (1910), Abderhaldens Fortschritte der naturwissenschaftlichen Forschung, 1; KOSTYTSCHEW (1911), Jahrb. wiss. Bot. 50. ([47]) WINOGRADSKI (1887), Botan. Ztg. 45; (1890-91) Annales Institut Pasteur, 4, 5; NIKLEWSKI (1907), Bull. acad. Cracovie; SÖHNGEN (1906), Cbl. Bakt. (II.) 15; cf. also the literature in ([23]); MEYERHOF, Pflügers Archiv f. Phys. 164-166. ([48]) Cf. CZAPEK, EULER and NATHANSOHN in ([6]); OPPENHEIMER, cited in ([41]); KRUSE (1910), Mikrobiologie; BENECKE (1912), Bau und Leben d. Bakterien, L. ([49]) BUCHNER, E. and H., and HAHN (1903), Die Zymasegärung, München; BUCHNER (1908), Biochem. Zeitschr.; FISCHER, A. (1903), Vorles. üb. Bakt. 2. Aufl. Jena; MAYER, AD. (1906), Lehrb. d. Agrikulturchemie, vol. iii. 6. Aufl. Heidelberg; EULER (1911), Zeitschr. für physiol. Chemie, 70; EULER and LINDNER (1915), Chemie der Hefe und der alkohol. Gärung, Lpzg. ([50]) MOLISCH (1914), Ztschr. f. Botan. 6; LEICK (1916), Biol. Centralbl. 36. ([51]) MOLISCH (1912), Leuchtende Pflanzen, Jena, 2. Aufl.

Development

([52]) PFEFFER (1904), Physiologie, 2; WINKLER (1913), Entwicklungsphysiologie in Handwörterb. d. Naturw. vol. iii. Jena.

Introductory Remarks.—([53]) SACHS (1873), Arb. bot. Inst. Würzburg, 1; BURKOM (1915), Proefschrift Utrecht (1913) K. Ak. Amsterdam. Proc. ([54]) SACHS (1882), Vorlesungen über Pflanzenphysiologie; BERTHOLD (1904), Unters. z. Physiol. der pflanzl. Organisation, Leipzig. ([55]) VÖCHTING (1878), Organbildung, Bonn; *ibid.* (1908), Untersuchung z. exp. Anatomie u. Pathologie, Tübingen; SIMON (1908), Jahrb. wiss. Bot. 45; Berichte bot. Ges. 26; GOEBEL (1902), Biolog. Centralbl. 22; NĚMEC (1905), Studien über Regeneration, Berlin; KORSCHELT (1907), Regeneration und Transplantation, Jena; MORGAN (1907), Regeneration; WINKLER (1913), Handwörterb. d. Naturw. Jena, vol. iii. "Entwicklungsphysiologie"; LINSBAUER (1915), Denkschr. d. Akad. Wien, 93. ([56]) KASSNER (1910), Zeitschr. f. Pflanzenkrankheiten, 20.

Factors of Development.—([57]) BLAAUW (1914 and 1915), Ztschr. f. Bot. 6 and 7; VOGT (1915), Ztschr. f. Bot. 7; SIERP (1918), Ztschr. f. Bot. 10. ([57a]) KLEBS (1917), Sitzb. Heid. Akad. math.-nat. Kl. ([58]) KÖRNICKE (1904), Ber. bot. Ges. 22;

(1915), Jahrb. wiss. Bot. 56; URSPRUNG (1917), Ber. bot. Ges. 35. ([59]) STAHL (1883), Jen. Zeitschr. f. Naturwiss. 16; NORDHAUSEN (1901), Jahrb. wiss. Bot. 37; Ber. bot. Ges. 30 (1912). ([59a]) VOECHTING (1918), Unters. z. exp. Anatomie u. Pathologie, Tübingen. ([59b]) SCHILLING (1915), Jahrb. wiss. Bot. 55. ([60]) KÜSTER (1911), Die Gallen der Pflanzen; (1916) Pathol. Pflanzenanatomie, Jena; MAGNUS (1914), Entstehung d. Gallen, Jena; MOLLIARD (1918), Botanisches Centralbl. 138. ([60a]) HEINRICHER (1916), Denkschr. Ak. Wiss. Wien, math.-nat. Kl. 93; BURGEFF (1909), Die Wurzelpilze der Orchideen, Jena. ([61]) GOEBEL (1880), Bot. Ztg. 38; *id.* (1908) Experimentelle Morphologie, Leipzig; VÖCHTING (1892), Die Transplantation, Tübingen; *id.* (1885) Jahrbücher f. wiss. Bot. 16. ([61a]) WINKLER (1908), Ber. d. bot. Ges. 26a; *id.* (1909) Zeitschr. f. Bot. 1; *id.* (1910), *ibid.* 2 and Ber. bot. Ges. 28; NOLL (1905), Sitzungsber. niederrh. Gesellschaft f. Natur- und Heilkunde; STRASBURGER (1907), Jahrb. wiss. Bot. 44; *id.* (1909), Ber. bot. Ges. 27; BUDER (1911), Zeitschr. f. Abstammungslehre, 5; MACFARLANE (1895), Transact. R. Soc. Edinb. 37; BAUR and WINKLER (1911), Zeitschr. f. Bot. 3; BAUR (1911), see ([60]); WINKLER (1912), Unters. über Pfropfbastarde, Jena; MEYER (1915), Zts. f. Abstammungslehre, 13. ([61b]) WINKLER (1916), Zts. f. Botan. 8; BURGEFF (1914–15), Flora, 107 and 108.

Course of Development.—([62]) SORAUER (1913), Pflanzenkrankheiten, Berlin, 4. Aufl. ([63]) PENZIG (1890), Pflanzenteratologie. ([64]) KÜSTER, E. (1916), Patholog. Pflanzenanatomie, Jena, 2. Aufl. ([65]) KLEBS (1912), Biolog. Centralbl. 32; *id.* (1914), Abh. Heidelb. Akad.; *id.* (1915), Jahrb. wiss. Bot. 56; KÜSTER (1918), Flora, 111; LAKON (1915), Biol. Cbl. 35; MUNK (1914), Biol. Cbl. 34; SIMON (1914), Jahrb. wiss. Bot. 54; WEBER (1915), Ber. bot. Ges. 34; KNIEP (1915), Die Naturwissenschaften, 3; VOLKENS (1912), Laubfall u. Lauberneuerung in d. Tropen, Berlin. ([66]) FISCHER, A. (1907), Ber. bot. Ges. 25; CROCKER and DAVIS (1914), Bot. Gaz. ([68]). ([67]) GASSNER (1915), Jahrb. wiss. Bot. 55; LEHMANN (1915), Zts. f. Bot. 7; (1913) *ibid.* 5; (1918) Ber. bot. Ges. 36; OTTENWÄLDER (1914), Zts. f. Bot. 6. ([68]) JOHANNSEN (1906), Ätherverfahren b. Treiben, Jena; MOLISCH (1909), Das Warmbad, Jena; JESENKO (1912), Ber. bot. Ges. 30; LAKON (1912), Zeitschr. f. Bot. 4; MÜLLER-THURGAU and SCHNEIDER-ORELLI, Flora, 101 and 104; WEBER (1916), Sitzungsber. Ak. Wien, i. 125. ([69]) Cf. GOEBEL (1908), Exp. Morphologie, Lpzg.; (1916) Biolog. Centralbl. 36; WINKLER, cited in ([52]). ([70]) WINKLER (1916), Zts. f. Bot. 8; GERASSIMOFF (1904), Bot. Cbl. Beih. 18 and Bull. Soc. Natur. Moscou; MARCHAL (1907 and 1909), Bull. acad. Belg. ([71]) KRAUS (1868), Jahrb. wiss. Bot. 7; SACHS (1903), Flora, 77; SIERP (1913), Jahrb. wiss. Bot. 53; KRAUS (1915), Sitzungsber. phys. med. Ges. Würzburg. ([72]) HABERLANDT (1913, 1914), Sitzungsber. Berliner Akad.; KARSTEN (1915 and 1918), Ztschr. f. Bot. 7 and 10; LAMPRECHT, Beitr. z. allg. Botanik, 1. ([73]) STRASBURGER (1898–99), Deutsche Rundschau; SCHENCK (1907), Wiss. Ergebnisse der Tiefsee Expedition, vol. ii. Heft 3, Jena. ([74]) KLEBS (1903), Willkürliche Entwicklungsänderungen, Jena; *id.* (1896), Fortpflanzungsphysiologie nied. Organismen, Jena; (1918) Flora, 111. ([75]) CORRENS (1907), Bestimmung und Vererbung des Geschlechts, Berlin; STRASBURGER (1909), cited in ([79]); (1910) Jahrb. wiss. Bot. 48; NOLL (1907), Sitzungsber. niederrh. Ges. ([76]) NOLL (1902), Sitzungsber. niederrh. naturf. Gesellsch.; EWERT (1907), Parthenokarpie . . . d. Obstbäume, Berlin; MÜLLER-THURGAU (1908), Landw. Jahrb. d. Schweiz. ([77]) FITTING (1909–10), Zeitschr. f. Bot. 1, 2; (1909) Biolog. Centralbl. 29. ([78]) Another view is held by SCHELLENBERG, Report of meeting of 15th Nov. 1907 of the Gesellschaft schweizerischer Landwirte. ([79]) WINKLER (1908), Progr. rei bot. 2; STRASBURGER (1909), Zeitpunkt der Bestimmung des Geschlechts,

Apogamie, Parthenogenesis, etc., Jena; ERNST (1918), Bastardierung als Ursache der Apogamie, Jena. ([80]) STRASBURGER (1905), Die stofflichen Grundlagen der Vererbung, Jena; CORRENS (1912), Die neuen Vererbungsgesetze, Berlin; HÄCKER (1911), Allgemeine Vererbungslehre, Braunschweig; JOHANNSEN (1909), Elemente der exakten Erblichkeitslehre, Jena; BAUR (1911), Einführung in die exp. Vererbungslehre, Berlin. On the whole subject consult the Zeitschrift für induktive Abstammungs- und Vererbungslehre, Berlin. ([81]) KÖLREUTER (1761–66), Vorl. Nachr. v. einigen d. Geschlecht d. Pflanzen betreffenden Versuchen und Beobachtungen (OSTWALDS Klassiker, No. 41); FOCKE (1881), Die Pflanzenmischlinge, Berlin; DE VRIES (1903), Die Mutationstheorie. ([82]) MENDEL (1901), Flora, 89 (OSTWALDS Klassiker, No. 121); CORRENS (1903), MENDELS Briefe an NÄGELI (Abh. Sächs. Ges. d. Wiss. 29); DE VRIES (1900), Berichte bot. Ges. 18; *id.* (1903), Die Mutationstheorie, Leipzig; CORRENS (1900), Berichte bot. Ges. 18; TSCHERMAK (1900), Zeitschr. f. landw. Versuchswesen in Österreich. ([83]) CORRENS (1918), Sitzungsber. Akad. Berlin. ([84]) ROSEN (1911), Beitr. z. Biologie, 10; *id.* (1913), Beitr. z. Pflanzenzucht, Heft 3; LEHMANN (1914), Zeitschr. f. ind. Abst. 13. ([85]) DARWIN (1868), Animals and Plants under Domestication; DE VRIES (1903), see ([82]); JOHANNSEN (1909), Elemente der exakten Erblichkeitslehre, Jena; BAUR (1914), Einf. in die Abstammungslehre, 2. Aufl. Berlin. ([86]) DE VRIES (1903), cited in ([82]); *ibid.* (1912) Die Mutationen in der Erblichkeitslehre, Berlin; KORSCHINSKY (1906), Flora, 89; WOLF (1909), Zeitschr. f. Abstammungslehre, 2; LEHMANN (1914), Naturwissenschaften, 2; HAENICKE (1916), Ztschr. f. Bot. 8. ([87]) DARWIN (1859), Origin of Species; KLEBS (1916), Zts. f. Abst. u. Vererbg. 17; LAMARCK (1809), Philosophie zoologique; LOTSY (1908), Vorlesungen üb. Deszendenztheorie, Jena; RENNER (1917), Zts. f. Abst. u. Vererbg. 18; LEHMANN (1918), Ztschr. f. Botanik, 10 (collected references).

Movement

([88]) PRINGSHEIM (1912), Reizbewegungen d. Pfl., Berlin; JOST (1913), Reizbewegungen in Handw. d. Naturwissenschaften, Jena, vol. viii. ([89]) ULEHLA (1911), Biolog. Centralbl. 31; BUDER (1915), Jahrb. wiss. Bot. 56. ([90]) MÜLLER (1908), Ber. bot. Ges. 27. ([91]) FECHNER (1915), Ztschr. f. Bot. 7; SCHMIDT (1918), Flora, 111. ([92]) ROTHERT (1901), Flora, 88; JENNINGS (1910), Das Verhalten der niederen Organismen, Lpzg.; BUDER (1915, 1917), Jahrb. wiss. Bot. 56, 58; NIENBURG (1916), Ztschr. f. Bot. 8; OLTMANNS (1917), Ztschr. f. Bot. 9. ([93]) SENN (1908), Die Gestalts- und Lageveränderungen der Pflanzenchromatophoren, Leipzig; (1919) Ztschr. f. Bot. 11. ([94]) PFEFFER (1884), Unters. Bot. Institut Tübingen, 1; ROTHERT (1901), Flora, 88; KNIEP (1906), Jahrb. wiss. Bot. 43; BRUCHMANN (1909), Flora, 99; SHIBATA (1911), Jahrb. wiss. Bot. 49; KUSANO (1909), Journ. Coll. of Agric. Tokyo, 2; PRINGSHEIM (1916), Zts. f. physiolog. Chemie, 97. ([95]) STEINBRINCK (1906), Biol. Centralbl. 26. ([96]) RENNER (1915), Jahrb. wiss. Bot. 56; URSPRUNG (1915), Ber. bot. Ges. 33. ([97]) PFEFFER (1893), Die Reizbarkeit d. Pfl. (Verh. d. Ges. d. Naturforscher); NOLL (1896), Sinnesleben d. Pflanze (Ber. Senckenberg. Gesellsch.); FITTING (1905–1907), Reizleitung (Ergebnisse d. Physiologie, 4, 5) and Jahrb. wiss. Bot. 44 and 45; JOST (1913), Reizbewegungen in Handwörterb. d. Naturw. Jena, vol. viii. ([98]) POLOWZOW (1909), Unters. über Reizerscheinungen, Jena; KNIEP (1916), Fortschr. d. Psychologie, 4.

Tropisms.—([99]) KNIGHT (1806), OSTWALDS Klassiker, 62; DUTROCHET (1824), Rech. sur la structure intime (OSTWALDS Klassiker, 154); HOFMEISTER (1863), Jahrb. wiss. Bot. 3; FRANK (1868), Beiträge z. Pflanzenphysiologie, Leipzig; SACHS (1874), Arb. bot. Inst. Würzburg, 1; (1879) *ibid.* 2; LUXBURG (1905),

Jahrb. wiss. Bot. 41; SCHOBER (1899), Anschauungen über Geotropismus seit Knight, Hamburg, Programm; FITTING (1905), Jahrb. wiss. Bot. 41; *id.* (1913), Handwörterb. d. naturw. Reizbewegungen, vol. viii. Jena; GILTAY (1910), Zeitschr. f. Botan. 2; ENGLER, A. (1918), Tropismen u. exzentrisches Dickenwachstum, Zürich. ([100]) SIMON (1912), Jahrb. wiss. Bot. 51; HARDER (1914), Ber. bot. Ges. 32. ([101]) JOST (1901), Botan. Ztg. 59; RISS (1915), Zeitschr. f. Botanik, 7. ([102]) SCHWENDENER (1881), Sitzungsber. Berlin. Akad.; WORTMANN (1886), Botan. Ztg. 44; NOLL (1892), Heterogene Induktion, Leipzig; *id.* (1901), Sitzungsber. niederrhein. Ges.; NIENBURG (1911), Flora, 102; BREMEKAMP (1912), Rec. trav. bot. néerland. 9; MIEHE (1915), Jahrb. wiss. Bot. 56. ([103]) NOLL (1892), Heterogene Induktion, Leipzig; NĚMEC (1900), Berichte bot. Gesellsch. 18; further, Jahrb. wiss. Bot. 36; *id.* Studien über Regeneration, Berlin, 1905; HABERLANDT (1900), Berichte d. bot. Gesellschaft, 18; also Jahrb. wiss. Bot. 38, 42, 44; BUDER (1908), Ber. bot. Gesellsch. 26; DARWIN (1899), Annals of Botany, 13; (1903) Proc. R. Soc. 71; (1904) *ibid.* 73 and British Assoc. Cambridge; NOLL (1902), Berichte bot. Ges. 20; (1905) Sitzungsber. niederrh. Gesellsch.; CZAPEK (1895 and 1898), Jahrb. wiss. Bot. 27, 32; FITTING (1905), cited in ([99]); ZIELINSKY (1911), Zeitschr. f. Bot. 3; KNOLL (1909), Sitzungsber. Wien. Akad. (I.) 118; BISCHOFF (1911), Beihefte botan. Cbl. 28; HABERLANDT (1914), Sitzungsber. Ak. Berlin; DEWERS (1914), Beih. bot. Cbl. 31; ZOLLIKOFER (1918), Ber. bot. Ges. 36. ([104]) RUTTEN-PEKELHARING (1910), Trav. botan. néerl. 7; MAILLEFER (1910), Bull. soc. vaudoise des sc. nat. 46; *id.* (1912), *ibid.* 48; FRÖSCHEL (1909), Naturw. Wochenschr.; TRÖNDLE (1913), Jahrb. wiss. Bot. 52; (1915) N. Denkschr. schweiz. nat. Ges. 51. ([105]) WIESNER (1878–80), Heliotrop. Erscheinungen (Denkschriften k. k. Akad. Wien); STAHL (1881), Kompasspflanzen, Jena; OLTMANNS (1892 and 1897), Flora, 75 and 83; E. PRINGSHEIM (1907–1909), Beitr. z. Biologie, 9; ARISZ (1911), Kon. Akad. Amsterdam. Proceed.; NOACK (1914), Zeitschr. f. Bot. 6; BUDER (1917), Jahrb. wiss. Bot. 58; KARSTEN (1918), Flora, 111; ENGLER, A., see ([99]); HEILBRONN (1917), Ber. bot. Ges. 35. ([106]) BLAAUW (1918), Med. van Landbouwhooge School Wageningen, 15. ([107]) OLTMANNS (1897), Flora, 83; PRINGSHEIM (1907–1908), Beitr. z. Biologie, 9 and 10; ARISZ (1915), Rec. des trav. bot. néerland. 12. ([108]) DARWIN (1881), Power of Movement in Plants; VÖCHTING (1888), Bot. Ztg. 46; ROTHERT (1894), Cohns Beitr. z. Biolog. 7; HABERLANDT (1905), Lichtsinnesorgane L.; *id.* (1916), Sitzb. Berl. Akad.; FITTING (1907), Jahrb. wiss. Bot. 44 and 45; KNIEP (1907), Biolog. Centralbl. 27; NORDHAUSEN (1907), Ber. bot. Ges. 25; GIUS (1907), Sitzungsber. Wien. Akad. 116; BOYSEN-JENSEN (1911), Acad. de Danemark, Bulletin; BLAAUW (1909), Die Perzeption des Lichtes, Nymwegen; VAN DER WOLK (1911), Proc. Akad. Amsterdam. ([109]) FITTING (1907), Jahrb. wiss. Bot. 44; BOYSEN-JENSEN (1911), Ber. bot. Ges. 31; PAAL (1914), Ber. bot. Ges. 32; (1918) Jahrb. wiss. Bot. 58. ([109a]) HABERLANDT (1916), Sitzungsber. Akad. Berlin; NORDHAUSEN (1917), Zts. f. Botan. 9. ([110]) MOLISCH (1889), Sitzungsanzeiger Wien. Akad.; MIYOSHI (1894), Flora, 78 and Botan. Ztg. 52; SAMMET (1905), Jahrb. wiss. Bot. 41; LILIENFELD (1905), Ber. bot. Ges. 23; SACHS (1872), Arb. bot. Inst. Würzburg, 1; MOLISCH (1883), Sitzungsber. Wien. Akad. 88; MOLISCH (1884), Sitzungsber. Wien. Akad. 90; POLOWZOW (1909), Untersuchungen über Reizerscheinungen bei den Pflanzen, Jena; PORODKO (1912), Ber. bot. Ges. 30. ([111]) DARWIN (1876), Climbing Plants; PFEFFER (1885), Unters. bot. Institut Tübingen, 1; FITTING (1903), Jahrb. wiss. Bot. 38; SCHENCK (1892), Beiträge zur Biologie der Lianen, Jena; PEIRCE (1894), Annals of Bot. 8. ([112]) STARK (1916), Jahrb. wiss. Bot. 57; (1917) Ber. bot. Ges. 35.

Nastic Movements.—([113]) KNIEP (1913), Handw. d. Naturw. Jena, vol. viii., Reizerscheinungen; LINSBAUER (1916), Flora, 109; GOEBEL (1916), Biol. Cbl. 36. ([114]) PFEFFER (1875), Periodische Bewegungen, Leipzig; *ibid.* (1907) Unters. über Entstehung d. Schlafbewegungen (Abh. K. Ges. d. Wiss. Leipzig); FISCHER (1890), Bot. Ztg. 48; OLTMANNS (1895), Bot. Ztg. 53; STAHL (1897), Bot. Ztg. 55; STOPPEL (1910), Zeitschr. f. Bot. 2; STOPPEL and KNIEP (1911), *ibid.* 3; ERBAN (1916), Ber. bot. Ges. 34. ([115]) PFEFFER (1915), Abh. Kgl. Gesellsch. Leipzig, 34; STOPPEL (1916), Ztschr. f. Bot. 8. ([116]) DARWIN (1876), Insectivorous Plants; CORRENS (1896), Bot. Ztg. 54; BENECKE (1909), Zts. f. Botanik, 1; HOOKER (1916), Bull. Torrey Club, 43. ([117]) BRÜCKE (1848), Archiv f. Anatomie u. Physiol. (OSTWALDS Klassiker, 95); BERT (1867–70), Mém. Soc. Bordeaux, Paris; PFEFFER (1873), Physiolog. Untersuchungen; HABERLANDT (1890), Das reizleitende Syst. d. Sinnpflanze, Leipzig; *id.* (1901), Sinnesorgane im Pflanzenreich, Leipzig; PFEFFER (1873), Jahrb. wiss. Bot. 9; FITTING (1903), Jahrb. wiss. Bot. 39 (1905, 1906), Ergebnisse d. Physiol. 4, 5; LINSBAUER (1908), Wiesner-Festschrift, Wien; LUTZ (1911), Zeitschr. f. Botanik, 3; BOSE (1913), Res. on Irritability of Plants, Bombay and Calcutta. ([118]) LINSBAUER (1914), Ber. bot. Ges. 32; BOSE, cited in ([117]). ([119]) STARK, see ([112]).

THALLOPHYTA, BRYOPHYTA, PTERIDOPHYTA, BY H. SCHENCK

([1]) ENGLER-PRANTL, Natürl. Pflanzenfamilien, vol. i.; LOTSY, Vorträge über botanische Stammesgeschichte, vol. i. 1907, vol. ii. 1909; L. RABENHORSTS Kryptogamenflora von Deutschland, Österreich und der Schweiz; PASCHER, Die Süsswasserflora Deutschl., Österreichs u. d. Schweiz. ([2]) KLEBS, Die Beding. der Fortpflanzung bei niederen Algen und Pilzen, 1896, and Jahrb. f. wiss. Botanik, vols. xxxii.-xxxiv., also Willkürl. Entwicklungsänd. bei Pflanzen, 1903.

Lower Thallophyta.—([3]) A. FISCHER, Vorlesung. über Bakterien, 1897, 2. Aufl. 1903; MIEHE, Bakterien, Leipzig, 2. Aufl. 1918; LEHMANN and NEUMANN, Bakteriologie; GÜNTHER, Bakteriologie; HEIM, Lehrb. d. Bakteriologie; LÖHNIS, Landwirtsch. bakteriolog. Praktikum, 1911; BENECKE, Bau und Leben der Bakterien, 1912; A. MEYER, Die Zelle der Bakterien, 1912; VIEHÖVER, Ber. deutsch. bot. Ges. vol. xxx. 1912, p. 443. ([3a]) BUDER (Thiospirillum), Jahrb. wiss. Bot. vol. lvi. 1915, p. 529. ([4]) MOLISCH, Die Purpurbakterien, Jena, 1907. ([5]) MOLISCH, Leuchtende Pflanzen, 2. Aufl. 1912. ([6]) VON FABER, Jahrb. wiss. Bot. vol. li. 1912, p. 283. ([7]) SORAUER, LINDAU, REH, Handbuch der Pflanzenkrankheiten, 1906; W. MAGNUS, Ber. deutsch. bot. Ges. vol. xxxiii. 1915, p. 96. ([8]) MIEHE, Ztschr. f. Hygiene u. Infekt. vol. lxii. 1908, p. 155. ([9]) KEIL, Schwefelbakterien, Diss. Halle a. S. 1912; MOLISCH, Die Eisenbakterien, 1910; LIESKE, Jahrb. f. wiss. Bot. vol. xlix. 1911, p. 91. ([10]) A. FISCHER, Unters. über den Bau der Cyanophyceen u. Bakterien, 1897, also Bot. Zeitg. 1905, p. 51; HEGLER, Jahrb. f. wiss. Bot. vol. xxxvi. 1901, p. 229; MASSART, Recueil de l'inst. bot. de Bruxelles, vol. v. 1902; BRAND, Ber. deutsch. bot. Ges. 1901, p. 152; 1905, p. 62, and Beihefte bot. Ztrbl. vol. xv. 1903, p. 31; FRITSCH, Beihefte bot. Zentrbl. vol. xviii. 1905, p. 194; OLIVE, Beihefte bot. Ztrbl. 1905, vol. xviii. p. 9; GUILLIERMOND, Revue génér. de bot. vol. xviii. 1906, p. 392; PRINGSHEIM, Die Naturwissenschaften, 1913, p. 495; FECHNER, Ztschr. f. Bot. vol. vii. 1915, p. 289; PIEPER, Dissert. Berlin, 1915; KLEIN, Anzeig. Akad. Wien, vol. lii. 1915. ([10a]) G. SCHMIDT, Flora, N.F. vol. xi. 1918, p. 327; R. HARDER, Ztschr. f. Bot. vol. x. 1918, p. 177. ([10b]) R. HARDER, Ztschr. f. Bot. vol. ix. 1917, p. 145. ([11]) OLTMANNS, Morphologie und Biologie der Algen, vol. i. 1904, vol. ii. 1905, and

Handwörterb. der Naturw. vol. i. ([12]) SENN, Ztschr. f. wiss. Zool. vol. xcvii. 1911, p. 605; F. DOFLEIN, Lehrbuch der Protozoenkunde, 4. Aufl. 1916; PASCHER, Ber. deutsch. bot. Ges. vol. xxix. 1911, p. 193, vol. xxxii. 1914, p. 136, vol. xxxiv. 1916, p. 440, and Archiv f. Protistenk. vol. xxv. 1912, p. 153, vol. xxxvi. 1915, p. 81; PASCHER, Flagellaten u. Rhizopoden in ihren gegenseitigen Beziehungen, 1917. ([12a]) LEMMERMANN, Ber. deutsch. bot. Ges. vol. xix. 1901, p. 247. ([12b]) LOHMANN, Archiv f. Protistenk. vol. i. 1902, p. 89; SCHILLER, Die Naturwissenschaften, vol. iv. 1916, p. 277. ([12c]) G. HAASE, Archiv f. Protistenk. vol. xx. 1910, p. 47; CH. TERNETZ, Jahrb. wiss. Bot. vol. li. 1912, p. 435. ([13]) LISTER, A Monograph of the Mycetozoa, 1894; HARPER, Bot. Gaz. vol. xxx. 1900, p. 217; PAVILLARD, Progressus rei bot. vol. iii. 1910, p. 496; PASCHER, Ber. deutsch. bot. Ges. vol. xxxvi. 1918, p. 359. ([14]) JAHN, Ber. deutsch. bot. Ges. 1911, p. 231. ([15]) WORONIN, Jahrb. f. wiss. Bot. vol. xi. 1878, p. 548; NAWASCHIN, Flora, 1899, p. 404; PROWAZEK, Arb. kais. Gesundheitsamt, vol. xxii. 1905, p. 396; MARCHAND, C. r. Acad. Paris, vol. cl. 1910, p. 1348; SCHWARTZ, Annals of Bot. vol. xxv. 1911, p. 791, and vol. xxviii. 1914, p. 227; JAHN, Ztschr. f. Bot. vol. vi. 1914, p. 875. ([16]) THAXTER, Bot. Gaz. vol. xiv. 1892, p. 389; vol. xxiii. 1897, p. 395, and vol. xxxvii. 1904, p. 405; QUEHL, Ctrbl. f. Bakt. vol. ii. 16, 1906, p. 9; VAHLE, *ibid.* vol. xxv. 1909, p. 178. ([17]) SCHÜTT, Die Peridin. der Planktonexpedition, 1895; SCHILLING, Flora, 1891, p. 220; BER. deutsch. bot. Ges. 1891, p. 199; JORGENSEN, Die Ceratien, Leipzig, 1911; KLEBS, Verh. nat. med. Verein Heidelberg, vol. ix. 1912, p. 369; SCHILLING, Die Dinoflagellaten in PASCHERS Süsswasserflora Deutschlands, 1913. ([18]) SCHÜTT, Das Pflanzenleben der Hochsee, 1893; GRAN, Das Plankton des norwegischen Nordmeeres, 1902; KARSTEN, Wiss. Ergeb. der deutschen Tiefsee-Expedition, 1898–99, 1905–1907. ([19]) KLEBS, cf. ([17]). ([20]) DIPPEL, Diatomeen der Rhein-Mainebene, 1905; VON SCHÖNFELDT, Diatomaceae Germaniae, 1907; O. MÜLLER, Ber. deutsch. bot. Ges. 1898–1909; HEINZERLING, Bibl. bot. Heft 69, 1908; MANGIN, Ann. sc. nat. 9e sér. vol. viii. 1908, p. 177; KARSTEN, Handwörterb. d. Naturw. vol. ii. p. 960; KARSTEN, Ztschr. f. Bot. vol. iv. 1912, p. 417. ([21]) GRAN, Die Diat. der arkt. Meere, Fauna arctica, vol. iii. 1904; KARSTEN, Ber. deutsch. bot. Ges. 1904, p. 544, and Wiss. Ergebn. der d. Tiefsee-Exped. vol. ii. 2. Teil, 1907, p. 496; P. BERGON, Bull. soc. bot. France, vol. liv. 1907, p. 327; PAVILLARD, Bull. soc. bot. France, vol. lxi. 1914, p. 164; SCHILLER, Ber. deutsch. bot. Ges. vol. xxvii. 1909, p. 351. ([22]) BENECKE, Jahrb. f. wiss. Bot. vol. xxxv. 1900, p. 585; KARSTEN, Flora, Ergzb. 1901, p. 404; RICHTER, Denkschr. Akad. Wien, vol. lxxxiv. 1909. ([23]) SAUVAGEAU, Station d'Arcachon, Travaux des labor. vol. ix. 1906, p. 49, and vol. x. 1907, p. 1. ([24]) W. WEST and G. S. WEST, A Monograph of the Brit. Desmid. vol. i. 1904; KAUFFMANN, Ztschr. f. Bot. 1914, p. 721. ([25]) LUTMAN, Bot. Gaz. vol. xlix. 1910, p. 241, and vol. li. 1911, p. 401; VAN WISSELINGH, Ztschr. f. Bot. vol. iv. 1912, p. 337. ([26]) TRÖNDLE, Ztschr. f. Bot. vol. iii. 1911, p. 593, and vol. iv. 1912, p. 721; KURSSANOW, Flora, vol. civ. 1911, p. 65.

Algae.—([27]) PASCHER, Hedwigia, vol. liii. p. 6. ([28]) KÜTZING, Tabulae phycologicae. ([29]) WOLLENWEBER, Ber. deutsch. bot. Ges. vol. xxvi. 1908, p. 238. ([30]) GOROSCHANKIN, Flora, 1905, p. 420. ([31]) GERNECK, Beihefte bot. Centralbl. vol. xxi.[2] p. 221; TREBOUX, Ber. deutsch. bot. Ges. vol. xxx. 1912, p. 69. ([32]) GRINTZESCO, Rev. génér. de bot. vol. xv. 1903, p. 5. ([33]) HARPER, Bull. Univ. Wisconsin, No. 207, 1908, p. 280. ([34]) PASCHER, Hedwigia, vol. xlvi. 1907, p. 265; VAN WISSELINGH, Beih. bot. Ctrbl. vol. xxiii. I. 1908. ([35]) ALLEN, Ber. d. bot. Gesellsch. 1905, p. 285. ([36]) HABERLANDT, Sitzb. Akad. Wien, vol. cxv. I. 1906, p. 1; SVEDELIUS, Ceylon Marine Biolog. Reports, No. 4, 1906.

(37) FREUND, Beih. bot. Ctrbl. vol. xxi. I. 1907, p. 55. (38) DAVIS, Bot. Gazette, vol. xxxviii. 1904, p. 81; HEIDINGER, Ber. deutsch. bot. Ges. vol. xxvi. 1908, p. 312. (39) SKOTTSBERG, Wiss. Erg. der schwed. Südpolarexpedition, vol. iv. Lief. 6, 1907, p. 80; FRYE, RIGG and CRANDALL, Bot. Gaz. vol. lx. 1915, p. 473. (40) SAUVAGEAU, Société sc. d'Arcachon, Station biol. 11e année, 1908, p. 65. (41) SAUVAGEAU, C. rend. Soc. de biolog. Paris, vol. lxii. 1907, p. 1082; SCHILLER, Internat. Revue der ges. Hydrobiol. vol. ii. 1909, p. 62; F. BORGESEN, The Species of Sargassum, Kopenhagen, 1914, and The Marine Algae of the Danish West Indies, Part II. 1914, p. 222. (42) HANSTEEN, Jahrb. f. wiss. Bot. vol. xxxv. 1900, p. 611; HUNGER, *ibid.* vol. xxxviii. 1903, p. 70; KYLIN, Ztschr. f. Bot. vol. iv. 1912, p. 540; KYLIN, Ztschr. f. phys. Chemie, vol. xciv. 1915, p. 337, and Ber. deutsch. bot. Ges. vol. xxxvi. 1918, p. 10; WILLE, Univers. Festschrift Christiania, 1897; SYKES, Annals of Bot. vol. xxii. 1908, p. 292; KNIEP, Internat. Revue der Hydrobiologie, vol. vii. 1914, p. 1. (43) YAMANOUCHI, Bot. Gaz. vol. xlviii. 1909, p. 380, and Bot. Ztrbl. vol. cxvi. 1911, p. 435; YAMANOUCHI, Bot. Gaz. vol. liv. 1912, p. 441. (44) KYLIN, Ber. deutsch. bot. Ges. vol. xxxv. 1917, p. 298. (45) WILLIAMS, Annals of Bot. vol. xi. 1897, p. 545, and vol. xviii. 1904, pp. 141 and 183, vol. xix. 1905, p. 531; LEWIS, Bot. Gaz. vol. l. 1910, p. 59; MOTTIER, Annals of Bot. vol. xiv. 1900, p. 163. (46) SAUVAGEAU, C. rend. Paris, vol. clxi. 1915, vol. clxii. 1916, vol. clxiii. 1917; KYLIN, Svensk. bot. Tidsk. vol. x. 1916, p. 551, vol. xii. 1918, p. 21; PASCHER, Ber. deutsch. bot. Ges. 1918, p. 246; KUCKUCK, *ibid.* 1917, p. 557. (47) YAMANOUCHI, Bot. Gaz. vol. xlvii. 1909, p. 173; NIENBURG, Flora, vol. ci. 1910, p. 167, and Ztschr. f. Bot. vol. v. 1913, p. 1; SAUVAGEAU (Cystoseira), Bull. stat. biol. d'Arcachon, 14. Jahrg. 1912; KYLIN, Ber. deutsch. bot. Ges. vol. xxxiv. 1916, p. 194; MEVES, Archiv f. mik. An. vol. xci. 1918, p. 272. (48) MOTTIER, Annals of Bot. vol. xviii. 1904, p. 245; STRASBURGER, Wiesner-Festschrift, 1908, p. 24; SCHENCK, Bot. Jahrb. f. System, vol. xlii. 1908, p. 1; OEHLKERS, Ber. deutsch. bot. Ges. vol. xxxiv. 1916, p. 223; GOEBEL, Flora, N.F. vol. x. 1918, p. 344. (48a) ERNST, Bastardierung als Ursache der Apogamie im Pflanzenreich, 1918. (49) WOLFE, Annals of Bot. vol. xviii. 1904, p. 607; YAMANOUCHI, Bot. Gazette, vol. xli. 1906, p. 425; KURSSANOW, Flora, vol. xcix. 1909, p. 311; SVEDELIUS, Ber. deutsch. bot. Ges. vol. xxxii. 1914, p. 48; SCHILLER, Österr. bot. Ztschr. 1913, No. 4; v. FABER, Ztschr. f. Bot. vol. v. 1913, p. 801; KYLIN, Ber. deutsch. Bot. Ges. vol. xxxv. 1917, p. 155. (49a) SVEDELIUS, Kgl. Svensk. Vetenskapsakad. Handl. vol. xliii. 1908, p. 76. (49b) SVEDELIUS, Ber. deutsch. bot. Ges. vol. xxxv. 1917, p. 225. (49c) LEWIS, Annals of Bot. vol. xxiii. 1909, p. 639, and Bot. Gazette, vol. liii. 1912, p. 236; KUCKUCK, Ztschr. f. Bot. vol. iii. 1911, p. 180; SVEDELIUS, Svensk. Bot. Tidskrift, vol. v. 1911, p. 260, and vol. vi. 1912, p. 239; RIGG and DALGITY, Bot. Gaz. vol. liv. 1912, p. 164; SVEDELIUS, Ber. deutsch. bot. Ges. 1914, p. 106; Svensk. bot. Tidsk. vol. viii. 1914, p. 1; Nova acta reg. soc. sc. Upsaliensis, ser. 4, vol. iv. 1915; KYLIN, Ber. deutsch. bot. Ges. 1916, p. 257; Ztschr. f. Bot. 1916, pp. 97 and 545. (50) KUCKUCK, Sitzb. Akad. Berlin, 1894, p. 983; STURCH, Annals of Bot. vol. xiii. 1899, p. 83; EDDELBÜTTEL, Bot. Ztg. 1910, p. 186.

Fungi.—(51) DE BARY, Vgl. Morphologie und Biolog. der Pilze, 1884 (English Translation). (52) BREFELD, Bot. Unters. über Schimmelpilze, Unters. aus dem Gesamtgebiet d. Mykologie, vols. i.-xv. 1872–1912; VON TAVEL, Vgl. Morphol. d. Pilze, 1892; E. FISCHER, Handwörterb. d. Naturw. vol. vii. p. 880; A. GUILLIERMOND, Progr. rei bot. vol. iv. 1913, p. 389. (53) BALLY, Jahrb. f. wiss. Bot. vol. l. 1911, p. 95, and Mykolog. Ctrbl. II. 1913, p. 289; GERTR. TOBLER, Die Synchytrien, Jena, 1913; KUSANO, Journ. College of Agric. Tokyo, 1912,

p. 141 ; G. SCHNEIDER, (Kartoffelkrebs) Deutsche landw. Presse, 1908, No. 79, and 1909, No. 88. (54) WORONIN, Mém. de l'Acad. imp. des Sciences de Saint-Pétersbourg, 1904, 8e sér. vol. xvi. No. 4, p. 1. (55) TROW, Annals of Bot. vol. ix. 1895, p. 609 ; vol. xiii. 1899, p. 130 ; vol. xviii. 1904, p. 541 ; KLEBS, Jahrb. f. wiss. Bot. vol. xxxiii. 1899, p. 513 ; DAVIS, Bot. Gaz. vol. xxxv. 1903, p. 233 ; CLAUSSEN, Berichte deutsch. bot. Ges. vol. xxvi. 1908, p. 144 ; MÜCKE, Berichte deutsch. bot. Ges. vol. xxvi.a 1908, p. 367. (56) WAGER, Annals of Bot. vol. iv. 1889–91, p. 127 ; vol. x. 1896, pp. 89 and 295 ; vol. xiv. 1900, p. 263 ; BERLESE, Jahrb. f. wiss. Bot. vol. xxxi. 1898, p. 159 ; DAVIS, Bot. Gaz. vol. xxix. 1900, p. 297 ; STEVENS, Bot. Gaz. 1899, vol. xxviii. p. 149 ; 1901, vol. xxxii. p. 77 ; 1902, vol. xxxiv. p. 420, and Ber. deutsch. bot. Ges. 1901, p. 171 ; TROW, Annals of Bot. vol. xv. 1901, p. 269 ; MIYAKE, Annals of Bot. 1901, p. 653 ; ROSENBERG, Bihang till Svensk. Ak. vol. xxviii. 1903 ; RUHLAND, Jahrb. f. wiss. Bot. vol. xxxix. 1904, p. 135 ; ROSTOWZEW, Flora, 1903, p. 405 ; KRÜGER, Ctrbl. f. Bakteriol. II. vol. xxvii. 1910, p. 186. (57) HARPER, Annals of Bot. vol. xiii. 1899, p. 467 ; GRUBER, Ber. deutsch. bot. Ges. 1912, p. 126 ; MCCORMICK, Bot. Gaz. vol. liii. 1912, p. 67!; MISS KEENE, Annals of Bot. vol. xxviii. 1914, p. 455. (57a) BLAKESLEE, Bot. Gaz. vol. xlii. 1906, p. 161 ; vol. xliii. 1907, p. 415, and vol. xlvii. 1909, p. 418 ; HAGEM, Vidensk. Selskab. Skrifter-Christiania, 1907, No. 7 ; BURGEFF, Ber. deutsch. bot. Ges. vol. xxx. 1912, p. 679, and Flora, vol. cvii. 1914, p. 259 ; vol. cviii. 1915, p. 440. (58) BLAKESLEE and GORTNER, Biochem. Bull. II. 1913, p. 542. (59) OLIVE, Bot. Gaz. vol. li. 1906, pp. 192 and 229. (60) RACIBORSKI, Flora, 1906, p. 106 ; FAIRCHILD, Jahrb. f. wiss. Bot. vol. xxx. 1897, p. 285. (61) HARPER, Jahrb. f. wiss. Bot. vol. xxx. 1897, p. 249, also Annals of Bot. vol. xiii. 1899, p. 467 ; vol. xiv. 1900, p. 321 ; GUILLIERMOND, Revue génér. de bot. vol. xvi. 1904, pp. 49 and 130 ; vol. xxxiii. 1911, p. 89 ; CLAUSSEN, Bot. Ztg. 1905, p. 1 ; MAIRE, C. r. soc. biol. vol. lviii. 1905, p. 726 ; FRASER and WELSFORD, Annals of Bot. vol. xxii. 1908, p. 465 ; OVERTON (Thecotheus), Bot. Gaz. vol. xlii. 1906, p. 450 ; W. BROWN, Bot. Gaz. vol. lii. 1911, p. 275. (62) BLACKMAN and WELSFORD, (Gnomonia) Annals of Bot. vol. xxvi. 1912, p. 761 ; NIENBURG, (Polystigma) Ztschr. f. Bot. vol. vi. 1914, p. 369 ; KILLIAN, (Venturia) Ztschr. f. Bot. vol. ix. 1917, p. 353 ; RAMLOW, (Ascoboleen) Mykol. Ctrbl. vol. v. 1914, p. 177 ; DODGE, Bull. Torrey Bot. Club, vol. xli. 1914, p. 157 ; KILLIAN, (Cryptomyces) Ztsch. f. Bot. vol. x. 1918, p. 49. (63) SCHIKORRA, Ztsch. f. Bot. vol. i. 1909, p. 379. (64) FRASER, Annals of Bot. vol. xxi. 1907, p. 349. (65) HARPER, Ber. deutsch. bot. Ges. 1895, p. 475, and Jahrb. f. wiss. Bot. vol. xxix. 1895, p. 655 ; NEGER, Flora, 1901, p. 333, and 1902, p. 221 ; SALMON, Annals of Bot. vol. xx. 1906, p. 187; HARPER, Carnegie Institution of Washington, publ. No. 37, 1902 (Phyllactinia). (66) FRASER and CHAMBERS, Annales mycolog. vol. v. 1907, p. 419. (67) MIEHE, Medic. Klinik, 1906, p. 943. (68) WEESE, Ztsch. f. d. landw. Versuchswesen Österreich, 1911 ; VOGES, Ctrbl. Bakter. vol. xxxix. 1914, p. 641. (69) HARPER, Annals of Bot. vol. xiv. 1900, p. 321 (Pyronema) ; CLAUSSEN, Bot. Ztg. 1905, p. 1 (Boudiera), and Berichte der deutsch. bot. Ges. 1906, p. 11 ; CLAUSSEN, (Pyronema) Ber. d. bot. Ges. 1907, p. 586, and Ztsch. f. Bot. vol. iv. 1912, p. 1. (70) KROMBHOLZ, Abb. u. Beschreib. der Schwämme, 1831–46 ; LENZ, Nützl. schädl. u. verdächt. Schwämme, 1890 ; GRAMBERG, Pilze der Heimat ; MICHAEL, Führer für Pilzfreunde ; RÖLL, Unsere essb. Pilze ; SYDOW, Taschenbuch der wichtigeren essbaren u. giftigen Pilze ; DITTRICH, Ber. deutsch. bot. Ges. vol. xxxiv. 1916, pp. 424 and 719 ; A. RICKEN, Vademecum für Pilzfreunde, 1918, and Die Blätterpilze (Agaricaceae) Deutschlands, 1915. (71) FISCHER, Bot. Ztg. 1908, p. 141 ; BUCHHOLTZ, Ann. mycol. vol. vi. 1908, p. 539 ; FISCHER, Ztschr. f. Bot. vol. ii. 1910, p. 718.

(72) GIESENHAGEN, Flora, Erzgb. 1895, p. 267, and Bot. Ztg. 1901, p. 115; IKENO, Flora, 1901, p. 229, and 1903, p. 1. (73) GUILLIERMOND, Rev. génér. de bot. 1903, p. 49; E. C. HANSEN, Ztrbl. f. Bakt. 2. Abt. vol. xii. 1904; GUILLIERMOND, Rev. génér. de bot. 1905, p. 337; MARCHAND, Rev. gén. bot. 1913, p. 207. (74) THAXTER, Mem. of Americ. Acad. Boston, 1896, and vol. xiii. 1908; FAULL, Annals of Bot. vol. xxvi. 1912, p. 325. (75) RUHLAND, Bot. Ztg. 1901, p. 187; FRIES, Ztschr. f. Bot. vol. iii. 1911, p. 145, and vol. iv. 1912, p. 792; KNIEP, Ztschr. f. Bot. vol. iii. 1911, p. 531. (76) HECKE, Ber. d. bot. Ges. 1905, p. 248; LANG, Ztrbl. f. Bakt. II. vol. xxv. 1910, p. 86; RAWITSCHER, Ztschr. f. Bot. vol. iv. 1912, p. 673, and Ber. deutsch. bot. Ges. vol. xxxii. 1914, p. 310; WERTH, Arbeit. kais. biol. Anst. vol. viii. 1911, p. 427; PARAVICINI, Ann. mycol. vol. xv. 1917, p. 57. (77) Many papers by P. MAGNUS, KLEBAHN, SYDOW, ERIKSSON, TISCHLER, E. FISCHER, LAGERHEIM, etc.; P. et H. SYDOW, Monographia Uredinarum; MAIRE, Progr. rei bot. vol. iv. 1911, p. 109. (78) BLACKMAN, Annals of Bot. vol. xviii. 1904, p. 323; BLACKMAN and FRASER, *ibid.* vol. xx. 1906, p. 35; CHRISTMAN, Bot. Gaz. vol. xxxix. 1905, p. 267; CHRISTMAN, Transact. Wisconsin Acad. vol. xv. 1907, p. 517, and Bot. Gazette, vol. xliv. 1907, p. 81; OLIVE, Annals of Bot. vol. xxii. 1908, p. 331; DITTSCHLAG, Ztrbl. f. Bakt. II. vol. xxviii. 1910; KURSSANOW, Ztschr. f. Bot. II. 1910, p. 81; WERTH and LUDWIGS, Ber. deutsch. bot. Ges. vol. xxx. 1912, p. 523; FROMME, Bot. Gaz. vol. lviii. 1914, p. 1; KURSSANOW, Ber. deutsch. bot. Ges. vol. xxxii. 1914, p. 317. (79) KLEBAHN, Die wirtswechselnden Rostpilze, 1904. (80) ERIKSSON and TISCHLER, Svenska Vet. Akad. Handl. 1904, vols. xxxvii. xxxviii; KLEBAHN, Ber. deutsch. bot. Ges. 1904, p. 255; E. FISCHER, Bot. Ztg. 1904, p. 327; MARSHALL WARD, Annals of Bot. vol. xix. 1905, p. 1. (81) HOFFMANN, Ztrbl. f. Bakt. 2. Abt. vol. xxxii. 1911; WERTH, *ibid.* vol. xxxvi. 1912. (81a) KUNKEL, Americ. Journ. of Bot. vol. i. 1914, p. 37. (82) KNOLL, Jahrb. wiss. Bot. vol. l. 1912, p. 453, and Ber. deutsch. bot. Ges. vol. xxx. 1912, p. 36. (83) H. KNIEP, Ztschr. f. Bot. vol. v. 1913, p. 593; vol. vii. 1915, p. 365; vol. viii. 1916, p. 353; Flora, N.F. vols. xi.-xii. 1918, p. 380. (84) R. HARTIG, Der echte Hausschwamm, 1885, ed. 2 by VON TUBEUF, 1902; MÖLLER and FALCK, Hausschwammforschungen, vols. i.-vi. 1907–1912; MEZ, Der Hausschwamm, Dresden, 1908; FALCK, Mykolog. Unt. u. Ber. I. 1913. (85) MÖLLER, Pilzgärten südamerik. Ameisen, 1893; HOLTERMANN, Schwendener-Festschrift, 1899; FOREL, Biolog. Zentralbl. 1905, p. 170; HUBER, Biol. Zentralbl. 1905, p. 606. (86) E. FISCHER, Denkschr. Schweiz. nat. Ges. vols. xxxii. and xxxvi.; MÖLLER, Brasil. Pilzblumen, 1895; ATKINSON, Bot. Gaz. vol. li. 1911, p. 1.

Lichens.—(87) WINKLER, Pfropfbastarde, 1. Teil, 1912, p. 102; TREBOUX, Ber. deutsch. bot. Ges. vol. xxx. 1912, p. 77; NIENBURG, Ztsch. f. Bot. 1917, p. 530. (88) ZOPF, Die Flechtenstoffe, 1907; STAHL, Häckel-Festschrift, 1904, p. 357. (89) BAUR, Flora, 1901, p. 319, also Bot. Ztg. 1904, p. 21; WOLFF, Flora, Ergzb. 1905, p. 31; NIENBURG, Flora, vol. xcviii. 1908, p. 1; F. BACHMANN, Annals of Bot. vol. xxvi. 1912, p. 747. (90) MÖLLER, Kultur flechtenbild. Ascomyceten, 1887, and Bot. Ztg. 1888, p. 421; GLÜCK, Flechtenspermogonien, Habilitationsschr. Heidelberg, 1899. (90a) FREDA BACHMANN, Arch. f. Zellforschung, vol. x. 1913, p. 369. (91) JOHOW, Jahrb. f. wiss. Bot. vol. xv. 1884, p. 361; MÖLLER, Flora, 1893, p. 254; POULSEN, Vid. Medd. Kopenhagen, 1899.

Bryophyta.—(92) GOEBEL, Organographie II. Bryophyten, 2. Aufl. 1915; Pteridophyten, 2. Aufl. 1918; CAMPBELL, The Structure and Development of Mosses and Ferns, 2nd ed. 1905; RABENHORST, Kryptogamenflora, vol. vi.; Lebermoose by K. MÜLLER, vol. iv.; Laubmoose by LIMPRICHT; LOESKE, Die Laubmoose Europas.

(93) GOEBEL, Flora, vol. xc. 1902, p. 279; DAVIS, Annals of Bot. vol. xvii. 1903, p. 477; HOLFERTY, Bot. Gaz. vol. xxxvii. 1904, p. 106; MELIN, Svensk. Bot. Tidskr. vol. x. 1916, p. 289; FLORIN, Svensk. Bot. Tidskr. vol. xii. 1918, p. 464. (94) ALLEN, Archiv f. Zellforschung, vol. viii. 1912, p. 179; WOODBURN, Annals of Bot. vol. xxvii. 1913, p. 93; WALKER, *ibid.* p. 116. (95) ZIELINSKI, Flora, vol. c. 1910, p. 1. (96) PFEFFER, Unters. bot. Inst. Tübingen, I. II.; LIDFORS, Jahrb. f. wiss. Bot. vol. xli. 1904, p. 65; ÅKERMAN, Ztschr. f. Bot. vol. ii. 1910, p. 94. (97) KREH, Nova Acta Acad. Leop. vol. xc. 1909, p. 214; CORRENS, Unt. über Vermehrung der Laubmoose durch Brutorgane und Stecklinge, Jena, 1899; BUCH, Brutorgane der Lebermoose, Dissert. Helsingfors, 1911. (98) SCHENCK, Bot. Jahrbücher f. Syst. vol. xlii. 1908, p. 1. (99) ANDREAS, Flora, 1899, p. 161; DOUIN, Rev. génér. de bot. vol. xxiv. 1912, p. 392; CLAPP, (Aneura) Bot. Gaz. vol. liv. 1912, p. 177; K. MEYER, (Corsinia) Bull. soc. imp. des nat. Moskau, 1911, p. 263, and Ber. deutsch. bot. Ges. vol. xxxii. 1914, p. 262; SCHIFFNER, Progressus rei bot. vol. v. 1917. (100) NĚMEC, Beihefte Bot. Ztrbl. vol. xvi. 1904, p. 253; GOLENKIN, Flora, vol. xc. 1902, p. 209; SCHIFFNER, Annales jard. Buitenzorg Supp. III.[2] 1910, p. 473; GARJEANNE, Flora, vol. cii. 1911, p. 147. (101) LANG, Annals of Bot. vol. xxi. 1907, p. 201; CAMPBELL, Annals of Bot. vol. xxi. 1907, p. 467, and vol. xxii. 1908, p. 91. (101a) PEIRCE, Bot. Gaz. vol. xlii. 1906, p. 55. (102) GOEBEL, Flora; vol. ci. 1910, p. 43; GEHRMANN, Ber. deutsch. bot. Ges. vol. xxvii. 1909, p. 341. (103) GARBER, Bot. Gaz. vol. xxxvii. 1904, p. 161; LEWIS, Bot. Gaz. vol. xli. 1906, p. 110; PIETSCH, Flora, vol. ciii. 1911, p. 347; BLACK, Ann. of Bot. vol. xxvii. 1913, p. 511. (104) HABERLANDT, Jahrb. f. wiss. Bot. vol. xvii. 1886, p. 359; TANSLEY and CHICK, Annals of Bot. vol. xv. 1901, p. 1; CORRENS, Vermehrung der Laubmoose, 1899; VAUPEL, Flora, 1903, p. 346; STRUNK, Diss. Bonn, 1914; GREBE, Studien zur Biol. u. Geogr. d. Laubmoose, Hedwigia, vol. lix. 1917. (105) K. GIESENHAGEN, Annals jard. Buitenzorg, Suppl. 3[2], 1910, p. 711. (106) ZEDERBAUER, Östr. bot. Ztschr. 1902; MERL, Flora, vol. cix. 1917, p. 189. (107) STEINBRINCK, Ber. deutsch. bot. Ges. vol. xxvi.a 1908, p. 410; vol. xxvii. 1909, p. 169, and vol. xxviii. 1910, pp. 19 and 549. (108) HABERLANDT, Jahrb. f. wiss. Bot. vol. xvii. 1880, p. 357; PORSCH, Der Spaltöffnungsapparat im Lichte der Phylogenie, 1905, p. 33. (109) BRYAN, Bot. Gaz. vol. lix. 1915, p. 40; MELIN, Svensk. bot. Tidskr. vol. x. 1916, p. 289. (110) DIHM, Flora, Ergzbd. 1894, p. 286; GOEBEL, Flora, 1895, p. 459; STEINBRINCK, Flora, Ergzbd. 1897, p. 131, and Biolog. Ztrbl. 1906, p. 727; KUNTZEN, Diss. Berlin, 1912. (111) ZIELINSKI, Flora, vol. c. 1909, p. 6.

Pteridophyta.—(112) BOWER, The Origin of a Land Flora, London, 1908. (113) PFEFFER, Unters. bot. Inst. Tübingen, vol. i. p. 363 (Farne, Selaginella); SHIBATA, Bot. Mag. Tokyo, vol. xix. 1905, p. 39 (Salvinia); *ibid.* pp. 79 and 126 (Equisetum); Ber. d. bot. Ges. 1904, p. 478, and Jahrb. f. wiss. Bot. vol. li. 1905, p. 561 (Isoëtes); LIDFORS, Ber. d. bot. Ges. 1905, p. 314 (Equisetum); BRUCHMANN, Flora, vol. xcix. 1909, p. 193 (Lycopodium); BULLER, Annals of Bot. vol. xiv. 1900, p. 543 (Farne); SHIBATA, Jahrb. wiss. Bot. vol. xlix. 1911, p. 1 (Equisetum, Farne, Salvinia, Isoëtes). (114) HANNIG, Flora, vol. cii. 1911, p. 209 and vol. ciii. 1911, p. 321. (115) HOOKER, Synopsis Filicum, 1883; BAKER, Fern Allies, 1887; CHRIST, Farnkräuter der Erde, 1897, and Die Geographie der Farne, Jena, 1910; CHRISTENSEN, Index Filicum, 1906. (116) CAMPBELL, Annal. Buitenzorg, vol. xxii. 1908, p. 99, and Suppl. 3[1], 1910, p. 69. (117) JEFFREY, Univers. of Toronto, Biolog. Series, No. 1, 1898 (Botrychium); BURLINGHAM, Bot. Gaz. vol. xliv. 1907, p. 34 (Ophiogl.); CHRYSLER, Annals of Bot. vol. xxiv. 1910, p. 1; LYON, Bot. Gaz. vol. xl. 1905, p. 455 (Botrychium). (118) STEINBRINCK, Biolog.

Ztrbl. 1906, p. 674, and Monatshefte für d. naturw. Unt. vol. xi. 1918, p. 131. ([119]) GOEBEL, Flora, vol. cv. p. 49. ([120]) SCHLUMBERGER, Flora, vol. cii. 1911, p. 383. ([121]) ARNOLDI, Flora, vol. c. 1909, p. 121; KUNDT, Beihefte Bot. Ztrbl. vol. 37[1], 1911, p. 26; ZAWIDZKI, Beihefte Bot. Ztrbl. vol. xxviii. 1912, p. 17; YASUI, Annals of Bot. vol. xxv. 1911, p. 469. ([121a]) PFEIFFER, Bot. Gaz. vol. liv. 1907, p. 445; OES, Ztschr. f. Bot. vol. v. 1913, p. 145. ([122]) F. SCHNEIDER, Beitr. z. Entw. der Marsiliaceen, Diss. Berlin, 1912; SHARP, Bot. Gaz. vol. lviii. 1914, p. 419; F. SCHNEIDER, Flora, vol. cv. 1913, p. 347. ([123]) STRASBURGER, Flora, vol. xcvii. 1907, p. 123. ([124]) STEINBRINCK, Biolog. Ztrbl. 1906, p. 724; HANNIG, Flora, vol. cii. 1911, p. 209; LUDWIGS, Flora, vol. ciii. 1911, p. 385; SHARP, Bot. Gaz. vol. liv. 1912, p. 89; VIDAL, Ann. sc. nat. 9[e] sér. vol. xv. 1912, p. 1. ([125]) BRUCHMANN, Flora, vol. ci. 1910, p. 220. ([125a]) HABERLAND, Beitr. z. allg. Bot. vol. i. p. 293. ([126]) BRUCHMANN, Flora, vol. civ. 1912, p. 180; vol. cv. 1913, p. 237, and Zeitschr. f. Bot. vol. xi. 1919, p. 39; LYON, Bot. Gaz. vol. xl. 1905, p. 285; CAMPBELL, Annals of Bot. vol. xvi. 1902, p. 419; DENKE, Beiheft z. bot. Ztrbl. vol. xii. 1902, p. 182; STEINBRINCK, Ber. deutsch. bot. Ges. 1902, p. 117, and Biolog. Ztrbl. 1906, p. 737; MITCHELL, Annals of Bot. vol. xxiv. 1910, p. 19; SYKES and STYLES, *ibid.* p. 523; WAND, Flora, vol. cvi. 1914, p. 237. ([127]) STEINBRINCK, Ber. deutsch. bot. Ges. vol. xxviii. 1910, p. 551, and vol. xxix. 1911, p. 334. ([128]) BRUCHMANN, Flora, 1905, p. 150; GOEBEL, Flora, 1905, p. 195. ([129]) W. SEYD, Zur Biolog. von Selag. Dissert. Jena, 1910; NEGER, Flora, vol. ciii. 1911, p. 74. ([130]) HABERLANDT, Ber. d. bot. Ges. 1905, p. 441. ([131]) STOCKEY, Bot. Gaz. vol. xlvii. 1909, p. 311.

Fossil Cryptogams.—([132]) Cf. the palaeophytological textbooks of W. PH. SCHIMPER, A. SCHENK, B. RENAULT, G. SAPORTA et MARION, SOLMS-LAUBACH, H. POTONIÉ, D. H. SCOTT, R. ZEILLER, A. C. SEWARD, W. JONGMANS. R. ZEILLER, Progressus rei bot. vol. ii. 1907, p. 171. ([133]) GORDON, Annals of Bot. vol. xxiv. 1910, p. 821. ([134]) OLIVER, Biol. Ztrbl. 1905, vol. xxv. p. 401, and Annals of Bot. vol. xxiii. 1909, p. 73; SCOTT, Wiss. Erg. Wiener bot. Kongr. 1905, p. 279; further, Progressus rei bot. vol. i. 1907, p. 139, and Smithsonian Report, 1907, p. 371; CHODAT, Archives sc. phys. et nat. 4[e] pér. vol. xxvi. Genève, 1908; OLIVER and SALISBURY, Annals of Bot. vol. xxv. 1911, p. 1.

SPERMATOPHYTA BY G. KARSTEN

Transition from Pteridophyta to Spermatophyta

([1]) W. HOFMEISTER, Vergleich. Unters. der Keim, Entfalt u. Fruchtbildung höherer Kryptogamen und der Samenbild. der Koniferen, Leipzig, 1851; HOFMEISTER, Higher Cryptogamia, London, 1862; E. STRASBURGER, Koniferen u. Gnetaceen, Jena, 1872; *id.* Angiospermen und Gymnospermen, Jena, 1879, and the comprehensive works: R. VON WETTSTEIN, Handbuch der systematischen Botanik, 2. Aufl. Leipzig and Wien, 1911; K. GOEBEL, Organographie der Pflanzen, 1. u. 2. Jena, 1898–1901 (English translation of 1st edition); and 2nd ed. 1. u. 2. 1913, 1918; J. M. COULTER and CH. J. CHAMBERLAIN, Morphology of Gymnosperms, Chicago, 1910, and Morphology of Angiosperms, Chicago, 1909. The above contain lists of literature, and only fundamental and historically important works or those giving more recent data are referred to here. ([2]) OVERTON, Reduktion der Chromosomen, Vierteljahrsschr. d. naturf. Ges. Zürich, 1893; E. STRASBURGER, Reduktionsteilung, Sitzber. K. A. d. W. Berlin, vol. xviii. 1904; *id.* Chromosomenzahlen und Reduktionsteilung, Pringsh. Jahrb. vol. xlv. 1908.

Morphology and Ecology of the Flower.—(2) PAYER, Organogénie de la fleur, 1857; BAILLON, Histoire des plantes, vols. i.-xiii. 1867–94; EICHLER, Blütendiagramme, 2 vols. Leipzig, 1875 and 1878; A. ENGLER and PRANTL, Natürl. Pflanzenfamilien, vols. ii.-iv. from 1889: *id.* Das Pflanzenreich from 1900; BERG and SCHMIDT, Atlas der offizinellen Pflanzen, 1863, and the second edition by A. MEYER and SCHUMANN, 1891–1902; further, the literature given under (1). (4) CHR. K. SPRENGEL, Das entdeckte Geheimnis der Natur, 1793 (OSTWALDS Klassiker, Nos. 48–51); CH. DARWIN, Ges. Werke, Übersetzung von CARUS, 1877, vols. ix. and x.; KNUTH, Handbuch der Blütenbiologie, 1898; O. KIRCHNER, Blumen und Insekten, Leipzig, 1911; G. TISCHLER, Das Heterostylie-Problem, Biol. Zentralbl. 38. 11. 1918; *id.* Festschrift HOHENHEIM, 254, 1918. (5) C. HESS, Exper. Unters. über den angeblichen Farbensinn der Bienen, Zoolog. Jahrb. vol. xxxiv. 1913; *id.* Münch. mediz. Wochenschrift, 1914, No. 27; *id.* Arch. f. d. ges. Physiologie, vol. clxiii. 1916; *id. ibid.* vol. clxx. 1918; K. VON FRISCH, Der Farbensinn und Formensinn der Biene, Zoolog. Jahrb. 35, 1914; *id.* Über den Geruchssinn der Biene, Zoolog.-bot. Ges. Wien, 68, 1918. The most recent works of the same author (Biolog. Zentralbl. 39, 3) could unfortunately not be consulted. (6) K. GOEBEL, Kleistogame Blüten, Biolog. Zentralbl. vol. xxiv. 1904; H. RITZEROW, Flora, 1907.

Development of the Sexual Generation.—(7) Cf. literature under (1), also SAKUGORO HIRASÉ, Ginkgo biloba, Journ. of the College of Science, Univ. imp. Tokio, vol. viii. 1895, and vol. xii. 1898; S. IKENO, Cycas revoluta, Jahrb. f. w. Bot. vol. xxvii. 1898; H. J. WEBBER, Spermatogenesis and Fecundation of Zamia, U.S. Dep. of Agricult. Washington, 1901; CH. J. CHAMBERLAIN, Fertilization and Embryogeny in Dioon edule, Bot. Gaz. vol. l. 1910; H. H. W. PEARSON, Some Observations on Welwitschia mirabilis, Philos. Transact. Royal Soc. 198, 1906; *ibid.* Further Observ. on Welwitschia, l.c. 200, 1909; *ibid.* On the Microsporangium and Microspores of Gnetum, etc., Ann. of Bot. 1912, vol. xxvi.; LANCELOT BURLINGHAM, Araucaria brasiliensis, Bot. Gaz. vol. lv. 1913; lvii. 1914; lix. 1915. (8) Literature under (1), also S. NAWASCHIN, Lilium Martagon., Bull. acad. imp. Saint-Pétersbourg, 1898; E. STRASBURGER, Doppelte Befruchtung, Bot. Ztg. 2. Abt. 1900; M. TREUB, Casuarina, Ann. Buitenzorg, vol. x. 1891; S. NAWASCHIN, Birke, Mém. acad. imp. Saint-Pétersbourg, 7e sér. vol. xlii. No. 12, 1894; *id.* Ulme, Bull. de l'acad. imp. d. sc. de Saint-Pétersbourg, 5e sér. vol. viii. No. 5, 1898; *id.* Corylus, *ibid.* vol. x. No. 4, 1899; *id.* Entw. d. Chalazogamen, Mém. acad. etc. 8e sér. vol. xxxi. No. 9, 1913; M. BENSON, Amentiferae, Transact. Linn. Soc. 2e sér. Bot. vol. iii. pt. 10, 1894; N. ZINGER, Cannabineen, Flora, vol. lxxxv. 1898; MODILEWSKI, Urticifloren, Flora, vol. xcviii. 1908; J. SCHWEIGER, Euphorbiaceen, Flora, vol. xciv. 1905; J. WOLPERT, Alnus u. Betula, Flora, vol. c. 1910; O. DAHLGREN, Plumbagella, Arkiv f. Bot. vol. xiv. 8, 1915, and Kg. Svensk. Vetensk. Handl. vol. lvi. 4, 1916; LULA PACE, Fertilization in Cypripedium, Bot. Gaz. vol. xliv. 1907. (9) J. HANSTEIN, Entwicklung des Keimes, Bot. Abhandl. vol. i. 1, 1870; E. STRASBURGER, Chromosomenzahlen, Vererbungsträger usw., Pringsh. Jahrb. vol. xlv. 1908; *id.* Apogamie, Parthenogenesis und Reduktionsteilung, Histolog. Beitr. vol. vii. 1909; HANS WINKLER, Parthenogenese u. Apogamie, Progr. rei bot. vol. ii. 1908; M. TREUB, Notes sur l'embryo, etc. (Avicennia), Ann. Buitenzorg, vol. iii. 1883; M. MERZ, Utricularien, Flora, vol. lxxxiv. 1897; BALICKA-IWANOWSKA, Gamopetales, Flora, vol. lxxxvi. 1899; F. BILLINGS, Beiträge zur Samenentwicklung, Flora, vol. lxxxviii. 1901; F. X. LANG, Polypompholyx u. Biblis, Flora, vol. lxxxviii. 1901; C. H. OSTENFELD and O. ROSENBERG, Hieracia, III.; O. ROSENBERG, Apogamy in Hieracium, Bot. Tidsskr. vol. xxviii.

1907; O. PORSCH, Phylogen. Erkl. d. Embryosackes u. d. dopp. Befr., Jena, 1907; F. A. F. C. WENT, Podostemaceen, I. and II. Verh. K. Akad. v. Wetensch. Amsterdam, 1910–12; *id.* Development of Podostemaceae, Extr. du recueil des travaux bot. néerlandais, vol. v. 1908; W. MAGNUS, Atypische Embryonal-Entw. der Podostemaceen, Flora, vol. cv. 1913. (10) A. ERNST, Bastardierung als Ursache der Apogamie, Jena, G. Fischer, 1918. (11) J. GAERTNER, De fructibus et seminibus plantarum, vols. i. and ii. Stuttg. 1789–91. (12) A. P. DE CANDOLLE, Pflanzenphysiologie; F. HILDEBRANDT, Verbreitungsmittel der Pflanzen, 1873; A. F. W. SCHIMPER, Pflanzengeographie, Jena, 1898; RUTGER SERNANDER, Myrmekochoren, Kg. Svensk. Vetensk. Handl. vol. xli. 1906; F. MORTON, Ameisen usw., Mitt. Nat. Ver. Univ. Wien, 1912. (13) G. KLEBS, Keimung, Untera. bot. Inst. Tübingen, vol. i. 536; J. LUBBOCK, Seedlings, vols. i. and ii. 1892; E. THEUNE, Biologie geokarper Pflanzen; F. COHNS, Beitr. vol. xiii. 1916.

Gymnospermae.—(14) Literature under (1), (3) and (7); K. GOEBEL, Pollenentleerung, Flora, Ergzbd. 1902, 237. (15) D. H. SCOTT, Palaeozoic Botany, in Progressus rei bot. vol. i. Jena, 1907; this contains the older literature; NEWELL ARBER, Origin of Angiosperms, Journ. Linn. Soc. vol. xxxviii. 263, 1907; G. R. WIELAND, American Fossil Cycads, 1906, Carnegie Inst. Washington; F. W. OLIVER, Physostoma elegans, Ann. of Bot. vol. xxiii. 1909; F. W. OLIVER and E. J. SALISBURY, Palaeozoic Seeds of the Conostoma Group, Ann. of Bot. vol. xxv. 1911; D. H. SCOTT, The Evolution of Plants, 1911, London; FERNAND PELOURDE, Les Progrès réalisés dans l'étude des Cycadophytes de l'époque secondaire, Progressus rei botanicae, vol. v. 2, 1916.

Angiospermae Dicotylae.—(16) Literature under (1) and (3), also H. HALLIER, Verwandtschaftsverhältnisse bei ENGLERS Rosalen, Parietalen, Myrtiflora usw., Abh. d. Naturw. Vereins Hamburg, 1903; this contains earlier views of the same author; E. SARGANT, Origin of Monocotyledons, Ann. of Bot. vol. xvii. 1903, and Bot. Gaz. vol. xxxvii. 1904; K. FRITSCH, Stellung der Monokotyledonen, Beibl. 79 in ENGLERS Bot. Jahrb. vol. xxxiv. 1905; E. STRASBURGER, Drimys, Flora, Ergzbd. 1905; NAWASCHIN, Chalazogamy, cf. (8); J. NITZSCHKE, Beitr. z. Phylogenie d. Monokotyledonen, 1914; COHNS, Beitr. vol. xii.; O. LIEHR, Ist die angenommene Verwandtschaft der Helobiae und der Polycarpicae auch in ihrer Zytologie zu erkennen? COHNS, Beitr. xiii. 1916. (17) L. DIELS, Käferblumen bei den Ranales und ihre Bedeutung für die Phylogenie der Angiospermen, Ber. deutsch. bot. Ges. 34, 1916; G. KARSTEN, Zur Phylogenie der Angiospermen, Zeitschr. f. Botanik, x. 1918, 369. (18) BÜSGEN, Fagales in KIRCHNER, LOEW, SCHROETER, Lebensgesch. d. Blütenpfl. vol. ii. 1, 1913. (19) H. Graf zu SOLMS-LAUBACH, Herkunft usw. des gew. Feigenbaums, Abh. d. K. Ges. d. W., Göttingen, 1882; FRITZ MÜLLER, Caprificus u. Feigenbaum, Kosmos, vol. vi. 1882; O. WARBURG, Kautschukpflanzen, Berlin, 1900; E. ULE, Kautschukpflanzen der Amazonasexped., ENGLERS Jahrb. vol. xxxv. 1905; K. GOEBEL, Schleuderfrüchte bei Urticifloren, Flora, vol. cviii. 1915. (20) J. SCHWEIGER, Euphorbiaceen, Flora, 94, 1905; A. MARKOWSKI, Gattg. Pedilanthus, Diss. Halle, 1912. (21) H. Graf zu SOLMS-LAUBACH, Cruciferenstudien, vols. i.-iv. Bot. Ztg. 1900–1906. (22) A. DE CANDOLLE, Ursprung der Kulturpflanzen, 1884; V. HEHN, Kulturpflanzen u. Haustiere, 7. Aufl. 1902; on *Bizarrien* cf. E. STRASBURGER, Pfropfhybriden; PRINGSHEIMS, Jahrb. vol. liv. 538, 1907. (23) MARLOTT, Kapland, Valvidia-Exped. vol. ii.[3] 1908; *id.* Mimicry among Plants, Transact. S. Afr. Philos. Soc. vols. xv. and xvi. 1904–1905. (24) K. GOEBEL, Bot. Ztg. 1882, 353; A. DE CANDOLLE, Origin of Cultivated Plants; H. Graf zu SOLMS-LAUBACH, Erdbeeren, Bot. Ztg. vol. i. 45, 1907; F. NOLL, Pfropfbastarde von Bronveaux,

Sitzber. niederrh. Ges. Bonn, 1906. ([25]) TH. BELT, Naturalist in Nicaragua, 1888, 218. ([26]) L. DIELS, Südwest-Australien, Veg. d. Erde, vol. vii. 1906. ([27]) F. TOBLER, Die Gattung Hedera, 1912. ([28]) P. GRAEBNER, Heide, Veget. d. Erde, vol. v. 1901; A. ARTOPOEUS, Ericaceen, Flora, 1903. ([29]) A. NESTLER, Cortusa Matthioli, Ber. deutsch. bot. Ges. 1912, 330. ([30]) R. VON WETTSTEIN, Ber. d. deutsch. bot. Ges. vol. xiii. 303; *id.* Deszendenztheor. Unters. I. Denkschr. k. k. Akad. d. W. Wien, 1900. ([31]) E. GILG, Strophanthus, Tropenpfl. 1902; *id.* H. THOMS, H. SCHEDEL, Ber. deutsch. pharmaz. Ges. 1904. ([32]) Cf. under ([19]), and also P. PREUSS, Exp. nach Zentral- u. Südamerika, Berlin, 1901; WARBURG, Kunene-Sambesi-Exped. Berlin, 1903. ([33]) M. TREUB, Ann. de Buitenzorg, vol. iii. 13, 1883. ([34]) HANS WINCKLER, Unters. über Pfropfbastarde, vol. i. 1912; *id.* Über experimentelle Erzeugung von Pflanzen mit abweichenden Chromosomenzahlen, Zeitschr. f. Botanik, vol. viii. 417, 1916. ([35]) E. HEINRICHER, Lathraea, Ber. deutsch. bot. Ges. 1893; *id.* Grüne Halbschmarotzer, i.-iv. Jahrb. f. w. Bot. 1897, 1898, 1901, 1902, 1909, 1910; R. VON WETTSTEIN, Monogr. Euphrasia, 1896; STERNECK, Alectorolophus, 1901. ([36]) K. GOEBEL, Morph. u. biolog. Studien 5, Ann. de Buitenzorg, vol. ix.; *id.* Flora, 1904, 98; E. MERL, Utricularien, Flora, vol. cviii. 1915. ([37]) M. TREUB, Myrmecodia, Ann. de Buitenzorg, iii. 129, 1883; H. MIEHE, Javanische Studien, Abh. Kg. Sächs. Ak. d. W. vol. xxxii. No. IV. Leipzig, 1911; F. C. VON FABER, Das erbliche Zusammenleben von Bakterien u. trop. Pflanzen, Jahrb. f. wiss. Bot. Lpzg. 1912, vol. li. 285; *id.* Die Bakteriensymbiose der Rubiaceen, *ibid.* vol. liv. 243, 1914. ([38]) F. NOLL, Cucurbitaceen, Landw. Jahrb. 30. Ergzbd. P. 1901; *id.* Parthenokarpie, Sitzber. niederrh. Ges. Bonn, 1902; G. BITTER, Bryonia, Abh. Nat. Ver., Bremen, 1904; C. CORRENS, Bestimmung u. Vererbung des Geschlechts, Berlin, 1907; J. KRATZER, Verwandtschaftliche Beziehungen der Cucurbitaceen, Flora, 110, 275, 1918. ([39]) L. JOST, Griffelhaare der Campanulaceen, Flora, Festschrift Stahl, vol. cxi. 1918. ([40]) K. MIYAKE, Wachstum des Blütenschaftes von Taraxacum, Beih. Bot. Zentralbl. vol. xvi. 3, 1904.

Monocotylae.—([41]) PETER STARK, Variabilität des Laubblattquirls bei Paris quadrifolia, Zeitschr. f. Botanik, vol. i. 1915; *id.* Blütenvariationen der Einbeere, Zeitschr. f. Abstammungs- u. Vererbungslehre xix. 1918. ([42]) K. GOEBEL, Streptochaeta, Flora, 1895, Ergzbd.; J. SCHUSTER, Grasblüte, Flora, vol. c. 1910; F. KOERNICKE, Handb. d. Getreidebaues, vol. i. Bonn, 1885; ALPH. DE CANDOLLE, Kulturpflanzen, Leipzig, 1884; G. SCHNEIDER, Vegetationsvers. mit 88 Hafersorten (bei 2 Sorten fehlt die Ligula), Landwirtsch. Jahrb. vol. xlii. 1913, p. 767 ff.; AUG. SCHULZ, Geschichte des Weizens, Zeitschr. f. Naturw. 1911; *id.* Geschichte des Spelzweizens, Abh. Naturf. Ges. Halle, 1917–18. ([43]) E. HANNIG, Pilzfreies Lolium, Bot. Ztg. 1907. ([44]) E. STRASBURGER, Verdickungsweise v. Palmen, Jahrb. f. w. Bot. vol. xxxiv. 1906; GR. KRAUS, Ann. de Buitenzorg, vol. xxiv. 1911; J. C. SCHOUTE, Dickenwachst. der Palmen, Ann. de Buitenzorg, vol. xxvi. Leiden, 1912. ([45]) G. TISCHLER, Parthenokarpe Angiosp.-Früchte, Jahrb. f. w. Bot. vol. lii. 1912; A. D'ANGREMOND, Parthenokarpie bei Bananen, Ber. deutsch. bot. Ges. vol. xxx. 1913; W. HERRMANN, Blattbewegung der Marantaceen, Flora, vol. cix. 1916, Diss. Jena; J. C. COSTERUS, Bau der Blumen von Canna und derjenigen der Marantaceen, Ann. de Buitenzorg, 2e sér. 15, 1916. ([46]) H. BURGEFF, Zur Biologie der Orchideen-Mykorrhiza, Diss. Jena, 1909. ([47]) H. FITTING, Beeinflussung der Orchideenblüte durch die Bestäubung usw., Zeitschr. f. Botanik, vol. i. 1909; *id.* Entwicklungsphysiol. Unters. an Orchideenblüten, Zeitschr. f. Botanik, vol. ii. 1910.

SYSTEMATIC INDEX

OF THE

OFFICIAL AND POISONOUS PLANTS

⊙ Official in Great Britain.
\+ Poisonous.
✲ Official and Poisonous.
* before the page indicates figure.

Thallophyta

✲ Claviceps purpurea, *444
\+ Boletus Satanas, *464
\+ Amanita muscaria, *465
\+ Amanita phalloides, *466
\+ Amanita mappa, *466
\+ Amanita verna, *466
\+ Russula emetica, 467
\+ Lactaria torminosa, 467
\+ Scleroderma vulgare, *467, 468

Pteridophyta

⊙ Dryopteris (Aspidium) filix mas, *507, 511
\+ Equisetum, *519, 522

Gymnospermae

\+ Taxus baccata, *593, *594, 602
⊙ Juniperus communis, *587, 602
\+ Juniperus sabina, *596, 602
⊙ Juniperus oxycedrus, 602
⊙ Abies balsamea, 602
⊙ Abies sibirica, 602
⊙ Pinus sylvestris, *601, 602

Quercifloræ

⊙ Quercus infectoria, 614

Urticinæ

⊙ Ficus carica, *618
⊙ Cannabis sativa, 619

Loranthifloræ

\+ Viscum album, *620

Piperinæ

⊙ Piper Betle, 623
⊙ Piper nigrum, *622, 623
⊙ Piper cubeba, *622, 623

Polygoninæ

⊙ Rheum, species of, 621

Hamamelidinæ

⊙ Liquidambar orientalis, 623
⊙ Hamamelis virginiana, 623

Tricoccæ

\+ Mercurialis annua, *623
\+ Euphorbia, species of, *624, 626
⊙ Croton Eleuteria, 627
⊙ Croton tiglium, 627
⊙ Ricinus communis, *625, *626, 627

Centrospermae

+ Agrostemma Githago, 627, *628
+ Saponaria officinalis, 627, *629
+ Anhalonium, species of, 629

Polycarpicae

+ Ranunculus sceleratus, *633, *634
+ Ranunculus arvensis, 633, *635
+ Caltha palustris, *636
+ Anemone pulsatilla, *635, 636
+ Anemone nemorosa, 636
+ Clematis, species of, 636
+ Helleborus, species of, 636
✲ Aconitum Napellus, *636, 637, 638
+ Aconitum lycoctonum, and other species, 637
⊙ Hydrastis canadensis, *638
✲ Delphinium staphisagria, 638
⊙ Illicium verum, 632
+ Illicium religiosum, 632
⊙ Myristica fragrans, *632
⊙ Podophyllum peltatum, 638, *639
⊙ Jateorhiza columba, 638
⊙ Cinnamomum Camphora, 639
⊙ Cinnamomum zeylanicum, 639
⊙ Cinnamomum Oliveri, 639
⊙ Aristolochia serpentaria, 639
⊙ Aristolochia reticulata, 639

Rhoeadinae

⊙ Papaver somniferum, 643
⊙ Papaver Rhoeas, *642, 643
⊙ Cochlearia armoracia, 646
⊙ Brassica nigra, *644, 646

Columniferae

⊙ Gossypium, species of, *648, 649
⊙ Theobroma cacao, *650, 651

Gruinales

⊙ Linum usitatissimum, *652
⊙ Guiacum officinale, 652
⊙ Guiacum sanctum, 652
⊙ Citrus Aurantium, var. Bigaradia, 654
⊙ Citrus medica, var. limonum, 654
⊙ Aegle marmelos, 654
⊙ Barosma betulina, 654
⊙ Pilocarpus jaborandi, 654
⊙ Picrasma excelsa, 654
⊙ Balsamodendron myrrha, 655
⊙ Polygala senega, *655

Sapindinae

+ Rhus toxicodendron, 655

Frangulinae

⊙ Rhamnus purshianus, 658

Rosiflorae

⊙ Rosa gallica, 664
⊙ Rosa damascena, 664
⊙ Prunus amygdalus, 664
⊙ Prunus domesticus, 664
⊙ Prunus serotina, 664
✲ Prunus laurocerasus, 664
⊙ Hagenia abyssinica, *662, 664
✲ Quillaja saponaria, *661, 664

Leguminosae

⊙ Acacia senegal, 668
⊙ Acacia arabica, 668
⊙ Acacia catechu, *666, 668
⊙ Acacia decurrens, 668
⊙ Cassia angustifolia, *666, 670
⊙ Cassia acutifolia, 670
⊙ Cassia fistula, 670
⊙ Copaifera Langsdorfii, 670
⊙ Tamarindus indica, *667, *668, 670
⊙ Haematoxylon campechianum, 670
⊙ Krameria triandra, *668, 670
+ Laburnum vulgare, *671
+ Coronilla varia, *673
+ Wistaria sinensis, 673
⊙ Astragalus gummifer, *672, 673
⊙ Glycyrrhiza glabra, 673
⊙ Spartium scoparium, 673
⊙ Andira araroba, 673
⊙ Pterocarpus santalinus, 673
⊙ Pterocarpus marsupium, 673
⊙ Myroxylon toluifera, 673
⊙ Myroxylon Pereirae, *669, *670, 673

Myrtiflorae

✲ Daphne Mezereum, 673, *674
✲ Daphne Laureola, 673
✲ Daphne Gnidium, 673
⊙ Eugenia caryophyllata, *676
⊙ Pimenta officinalis, 676
⊙ Melaleuca leucadendron, 676
⊙ Eucalyptus globulus, 676

Umbelliflorae

+ Hedera helix, 678
+ Conium maculatum, *683
⊙ Ferula foetida, 683
⊙ Dorema ammoniacum, 683
⊙ Pimpinella anisum, 683
⊙ Coriandrum sativum, 683
⊙ Foeniculum capillaceum, 683
⊙ Carum carvi, *679, 683

⊙ Anethum (Peucedanum) graveolens, 683
+ Cicuta virosa, *680
+ Sium latifolium, 682
+ Oenanthe fistulosa, *681
+ Aethusa cynapium, *682
+ Berula angustifolia, 682

Ericinae

⊙ Gaultheria procumbens, 686
⊙ Arctostaphylos Uva ursi, *684, 686
+ Rhododendron, 685
+ Ledum, 685

Diospyrinae

⊙ Styrax Benzoin, 686

Primulinae

+ Cyclamen europaeum, *686, 687
+ Anagallis arvensis, *686, 687
+ Primula obconica, 687
+ Corthusa matthioli, 687

Contortae

⊙ Olea europaea, *688
✱ Strychnos nux-vomica, 688, *689
⊙ Gelsemium nitidum, 688
⊙ Gentiana lutea, 689, *690
⊙ Swertia chirata, 689
+ Menyanthes trifoliata, 689
⊙ Strophanthus kombe, 689
⊙ Strophanthus hispidus, 689, *692
+ Nerium Oleander, 689, *691
+ Vincetoxicum officinale, 690, *693
⊙ Hemidesmus indicus, 690

Tubiflorae

⊙ Exogonium purga, *693
⊙ Ipomoea hederacea, 693
⊙ Ipomoea orizabensis, 693
⊙ Ipomoea turpethum, 693
⊙ Convolvulus Scammonia, 693
⊙ Rosmarinus officinalis, 696
⊙ Lavandula vera, *695, 696
⊙ Mentha piperita, 696
⊙ Mentha viridis, 696
⊙ Mentha arvensis, 696
⊙ Thymus vulgaris, 696
⊙ Monarda punctata, 696

Personatae

+ Nicotiana tabacum, 699, *700
+ Lycopersicum esculentum, 697
+ Solanum dulcamara, *697
+ Solanum tuberosum, 697
+ Solanum nigrum, 696
⊙ Capsicum minimum, 703
+ Atropa Belladonna, *698, 703
+ Datura stramonium, 697, *699, 703
+ Hyoscyamus niger, *701, 703
⊙ Digitalis purpurea, *702, 704
⊙ Picorhiza kurroa, 704
⊙ Plantago ovata, 704

Rubiinae

⊙ Cinchona succirubra, *705, *706
⊙ Uragoga Ipecacuanha, 705, *708
⊙ Ourouparia gambir, 705
⊙ Viburnum prunifolium, 706
⊙ Valeriana officinalis, 706, *708

Synandrae

⊙ Lobelia inflata, *711
⊙ Citrullus Colocynthis, 709, *710
⊙ Anacyclus Pyrethrum, 718
⊙ Artemisia maritima, 718
⊙ Anthemis nobilis, 718
⊙ Taraxacum officinale, 718
⊙ Arnica montana, *717, 718
⊙ Grindelia camporum, 718

Liliiflorae

✱ Colchicum autumnale, *722, 726
+ Schoenocaulon officinalis, 725
⊙ Aloe, species of, *724, 725, 726
⊙ Urginea scillae, 726
⊙ Urginea indica, 726
+ Paris quadrifolia, *727
+ Veratrum album, 725, 726
+ Convallaria majalis, 726

Glumiflorae

+ Lolium temulentum, 735, *738
⊙ Triticum sativum, 735
⊙ Oryza sativa, 735, *736
⊙ Zea mais, 735
⊙ Agropyrum repens, 735

Spadiciflorae

+ Arum maculatum, 741, *743
+ Calla palustris, 741

Scitamineae

⊙ Zingiber officinale, *744, 745
⊙ Elettaria cardamomum, 745

INDEX

(*Asterisks denote Illustrations*)

Abies, *598, 599, 602, 606
Abietineae, 597 ; generative nuclei, 566
Abscis layer, 119, 163
Absorbent roots, 184
Acacia, *171, *664, *665, 667 ; seedling of, *118
Accessory shoots, 121
Acer, *656 ; bud, *106
Aceraceae, 657
Acetabularia, 404, *406
Achillea, 717'; gynaeceum of, *548
Achlya, *432
Achnanthes, 391
Aconitum, *633, 636, *637, 638 ; gynaeceum of, *548
Acontae, 393
Acorus, 740, *742 ; flower of, *545 ; root of, *135
Acrasieae, 385
Acrocarpi, 496
Acrocomia, fruit of, *588
Actaea, 638
Actinomorphic, 72
Adaptations, 295 ; origin of, 210
Adonis, *633
Aecidia, 455
Aecidium Euphorbiae, 294
Aegle, 654
Aerenchyma, 49, 167
Aerobes, 275
Aerotaxis, 331
Aerotropism, 352
Aesculus, 657
Aestivation, 87
Aethalium, 384
Aethusa, *682
Agar-Agar, 427
Agaricineae, 465
Agaricus, *464, 467
Agathis, 597, 598
Agave, 726
Aglaozonia, 414
Agrimonia, 661
Agropyrum, 735
Agrostemma, 627, *628
Agrostis, 734
Aira, 734
Aizoaceae, 627
Ajuga, 695
Akrogynae, 489
Albugo, 432, *433, 434
Albumen crystals, 32
Albuminous substances, 266
Alchemilla, 661 ; flower, *550
Alcoholic fermentation, 275
Alder, *Alnus glutinosa*
Alectorolophus, 704
Aleurone grains, 30, *31
Alisma, 719, 721 ; embryo of, *576
Alismaceae, 719
Alkaloids, 29, 268
Alkanet, *Anchusa*
Allium, 725 ; root of, *135, 137
Allogamy, 201, 558
Almond, *Prunus Amygdalus*
Alnus, 610, *611 ; nodules, 261
Aloë, *724, *725 ; epidermis of, *169
Alopecurus, 734
Alpinia, 745
Alsophila, 506, *506, *509
Alstonia, 689
Alternation of generations, 193, 475 ; scheme of, 543
Althaea, *647, 649
Aluminium, 240
Amanita, *465, *466, 467
Amarantus, 95
Amaryllidaceae, 726
Amicia, day-position, *358 ; night-position, *358
Amides, 29
Amino-acids, 266
Amitotic division, 24
Ammonia, assimilation of, 257
Amoeboid movements, 328
Ampelopsis, *658
Amphibious plants, 293
Amphithecium, 481

Anabaena, 378
Anacardiaceae, 655
Anacyclus, 718
Anaerobes, 275
Anagallis, *686, 687; pyxidium, *583
Anakrogynae, 489
Ananassa, 730
Anaphase, 23
Anaptychia, spermogonium, *473
Anastatica, 333, 645
Anatropous ovule, 539, *540
Anchusa, 694
Andira, 673
Andreaea, *491, 494
Andreaeales, 494
Androecium, 546
Andromeda, 685
Andropogon, 734
Aneimia, *509
Anemone, *635, 636
Anemophilous plants, 552
Anethum, 682, 683
Aneura, 81, 488
Angiopteris, 503
Angiospermae, systematic arrangement, 606
Angiosperms, 542; flower, 545; fossil, 749; macrospores, 571; microspores of, 570
Anhalonium, 629
Animals, distribution of fruits by, 586
Anise, *Pimpinella Anisum*
Anisophylly, 116, *117
Annual rings, 153
Annularia, *521, 522
Annulus, 334, 508
Anonaceae, 632
Antennaria, 716
Anthemis, 717
Anther, 540, 546
Antheridial mother cell, 542
Antheridium, *199, *201, 369
Anthoceros, 477, *484
Anthocerotales, 483
Anthoclore, 29
Anthocyanins, 29
Anthophaeine, 29
Anthoxanthine, 29
Anthoxanthum, 734
Anthriscus, 682; flower of, *559
Anthurium, 740
Anthyllis, 672
Anticlinal cell walls, 307
Antirrhinum, 703; capsule, *583
Ants, distribution of seeds by, 587
Apical cell, 46, 78, 79, 85, 131
Apium, 682
Apocarpous gynaeceum, 547
Apocynaceae, 689
Apogamy, 202, 316, 511, 578; in *Marsilia*, 517
Apospory, 511, 578
Apothecium, 439
Apple, *Pyrus malus*
Apposition, growth by, 35
Apricot, *Prunus armeniaca*
Aquifoliaceae, 655
Aquilegia, *633, 637
Araceae, 740
Arachis, 672, 673
Araliaceae, 678
Araucaria, 597, 598, 599; prothallial cells, 566
Archaeocalamites, *521, 522
Archangelica, 682
Archegoniatae, 367
Archegonium, *201, *511
Archidium, 496
Archimycetes, 429
Arctostaphylos, *684, 685, 686
Arcyria, *382
Areca, 740
Arenga, 740
Argemone, 642
Arillus, 582
Aristolochia, *95; flowers of, *561; pollination of, 556, 560; vascular bundle, *145
Aristolochiaceae, 639
Armeria, *549
Armillaria, 466; basidium, *452; clamp formation, *462
Arnica, *712, *713, *717, 718
Arrhenatherum, 734
Artemisia, *715, 718
Artichoke, *Cynara Scolymus*
Artificial system, 365
Artocarpus, 618
Arum, 741, *743
Ascent of water, 236
Asclepiadaceae, 689
Asclepias, *693
Ascodesmis, 438
Ascolichenes, 471
Ascomycetes, 437; asexual reproduction, 439; sexual organs, 438
Ascus, 437, 439
Asexual reproductive cells, 195
Ash, *Fraxinus*
Ash of plants, constituents of, 221, 238
Asparagin, 258
Asparagus, 725
Aspergillaceae, 441
Aspergillus, 438, 441, *442; conidiophore, *196
Asperula, 704
Aspidistra, pollination of, 558
Aspidium, *497, 506, *507, 511
Asplenium, development of the sporangium of, *500
Assimilated material, quantity of, 253; transformation of, 263; translocation of, 263

Assimilation, 247; amount of, 254; of carbon dioxide, products of, 252
Assimilation experiment, *253
Aster, 716
Asteroxylon, 501
Astragalus, *672, 673
Atriplex, 627
Atropa, 697, *698, 699, 703
Atropous ovule, 539, *540
Attaching roots, 184
Auricularia, 460
Auricularieae, 460
Autogamy, 201
Autonomy of characters, 822
Autotrophic cormophytes, 165
Autumn Crocus, *Colchicum autumnale*
Autumn wood, 153, 154
Auxanometers, 278, *279
Auxiliary cells, 425
Auxospores, 389, *391
Avena, 734
Avicennia, 694
Axillary buds, 121
Azolla, 513, 515
Azotobacter, 259
Azygospores, 435

Bacillariaceae, 387
Bacillus, 370, *371, *372, 373, 374
Bacillus radicicola, 260
Bacteria, *74, 370; pathogenic, 374
Bacterioids, *260
Bacterium, 370
Balsamodendron, 655
Bambusa, 730, 734
Banana, *Musa*
Banyan, *Ficus bengalensis*
Bark, 59; formation of, 163
Barley, *Hordeum vulgare*
Barosma, 654
Bartsia, 191, 259, 704
Basidiobolaceae, 436
Basidiobolus, 428, 436
Basidiolichenes, 474
Basidiomycetes, 451
Basidiospores, 451, 455
Basidium, 437, 451, 455
Bast, 68, 158
Bast fibres, 158
Batrachium, 636
Batrachospermum, 423, *424, *425
Beaked Parsley, *Anthriscus*
Beech, *Fagus sylvatica*
Beet, *Beta vulgaris*
Beetles, pollination of flowers by, 607
Beggiatoa, 371, 376
Begonia, 195; regeneration, *283, *285
Bennettitaceae, 605
Bennettites, *605, *606
Benthos, 74
Berberidaceae, 638
Berberis, 638
Berry, 584
Berula, 682
Beta, 627
Betula, 610, *611
Betulaceae, 609
Biddulphia, *390
Bignoniaceae, anomalous secondary growth, *183
Biogenetic law, 209
Bird's-Foot, *Ornithopus sativus*
Bird's-foot Trefoil, *Lotus*
Bird's-nest Orchid, *Neottia*
Bitter principles, 29
Bitter-sweet, *Solanum dulcamara*
Blackberry, *Rubus*
Black Currant, *Ribes nigrum*
Black Mustard, *Brassica nigra*
Blaeberry, *Vaccinium myrtillus*
Blasia, 80, *81, *488, 489
Bleeding, 234
Blue-green Algae, *Cyanophyceae*
Bocconea, 642
Boehmeria, 619
Bog-Bean, *Menyanthes*
Bog Mosses, *Sphagnaceae*
Boletus, *464
Borage, *Borago*
Boraginaceae, 694
Borago, *694
Bordered pit, *67
Bostryx, *130
Boswellia, 655
Botrychium, *504, 505
Botrydium, *408
Boudiera, 438, *447
Bovista, 468
Bowenia, 589
Bracteal leaves, 118
Bracteole, 123
Branching, 75; cymose, 76, 127; dichotomous, 75, *76; false, 76, *78; lateral, 75, *76; monopodial, 126; racemose, 125; of the root, 138
Branch system, construction of, 123
Brassica, *643, *644, 645
Briza, 734
Broad Bean, *Vicia Faba*
Bromeliaceae, 730
Bromus, 734
Brown Algae, *Phaeophyceae*
Bruguiera, 674
Bryales, 494
Bryonia, 709; pollen, *541
Bryony, *Bryonia*
Bryophyllum, 195, 658
Bryophyta, 80, 475; antheridia, 477; archegonia, 478; fossil, 482; phylogeny, 481; sexual reproduction, 200; sporogonium, 480
Bryopsis, 406, 407

Buckwheat, *Fagopyrum esculentum*
Bud, 86, *88, *89, 176
Bud-scales, 176, 308
Bugloss, *Echium*
Bulbils, 194
Bulbochaete, 403, *405
Bulbs, 179, 194
Bundle sheath, 102
Burdock, *Lappa*
Burnet-Saxifrage, *Pimpinella*
Burseraceae, 655
Butea, 673
Butomus, 719, 721
Butter-Bur, *Petasites officinalis*
Buttress-roots, 140

Cabomba, *631, 632
Cactaceae, 628
Caeoma, 460
Caesalpiniaceae, 668
Cakile, 646
Calamagrostis, 734
Calamariaceae, 502, 522
Calamostachys, *521, 522
Calamus, 740
Calcium oxalate, 30
Calendula, 718
Calla, 741 ; pollination of, 558
Callithamnium, 422, *424
Callitris, 606
Callose, 64
Calluna, 686
Callus, 64, 159, 164, 298 ; wood, 164
Calobryum, 489
Caltha, *636
Calycanthus, 630
Calyptra, 131
Calyptrosphaera, *379
Calystegia, 693
Calyx, 546
Cambial cells, shape of, *146
Cambium, 47, 100, 142, *145, 147 ; fascicular, 144 ; interfascicular, 144 ; repeated formation of, 148 ; in root, 147
Campanula, 709, *711
Campanulaceae, 709
Campylotropous ovule, *540
Canadian Water-weed, *Elodea canadensis*
Canarium, 655
Cane-sugar, 252, 265
Canna, *746 ; flower of, *552
Cannabinaceae, 618
Cannabis, 618, 619
Cannaceae, 745
Cantharellus, 466
Caoutchouc, 268, 626, 689
Capillitium, 382
Capitulum, 127
Capparidaceae, 646
Capparis, *171, 646
Caprificus, 556
Caprifoliaceae, 705
Capsella, *643, 646 ; embryo of, *576 ; seed, *581
Capsicum, 697, 703
Capsule, loculicidal, 583 ; poricidal, 583 ; septicidal, 583
Carbohydrates, hydrolysis of, 264 ; fermentations of, 275
Carbon, 221
Carbon dioxide, 245, 247 ; assimilation of, 247
Cardamine, 195, *643
Cardinal points, 219
Carduus, *712, *718
Carex, 731, *732
Carnivorous plants, 185, 258
Carotin, 18
Carpels, 198, 539, 547
Carpinus, 611, *612
Carpodinus, 689
Carpogonium, 424
Carpospores, 424
Carrageheen, 427
Carrot, *Daucus*
Carroway, *Carum Carvi*
Carum, *679, 681, 683
Caruncula, 582, 624
Carya, 609
Caryophyllaceae, 627
Caspary's band, 57, *58
Caspary's dots, 135
Cassia, *666, 668, 670
Cassytha, 639
Castanea, 612, *614
Castilloa, 618
Casuarina, chalazogamy, 573
Catkin, *126
Cattleya, 749
Caulerpa, 195, *406
Cauliflory, 651
Cecidia, 295
Cedrus, 606
Celandine, *Chelidonium majus*
Celery, *Apium*
Cell-budding, 26
Cell division, 21, *22 ; causes of, 307 ; a process of reproduction, 310
Cell fusions, 44, 69
Cell plate, 24
Cell sap, 12, 28
Cell wall, 34 ; anticlinal, 47 ; chemical nature of, 37 ; periclinal, 47
Cells, constituent parts of, 11 ; embryonic, *11 ; form and size of, 10
Cellular plants, 366
Cellulose, 37 ; as a reserve substance, 265
Celtis, 617
Centaurea, 713 ; seismonastic movements, *362

Centaury, *Erythraea*
Central cylinder, 92, 94
Centriole, 12
Centrospermae, 627
Cephalanthera, 746
Cephalotaceae, 639
Cerastium, 627
Ceratiomyxa, 384
Ceratium, *387
Ceratocorys, *387
Ceratonia, 670
Ceratozamia, 589, *591
Cerbera, 689 ; fruit of, *586
Cercis, *666, 670
Cereus, *174, 629, *630
Ceriops, 674
Cetraria, *469, 471, *472, 474
Chaerophyllum, 682
Chaetocladium, 435
Chalaza, 539
Chalazogamy, 573
Chamomile, *Matricaria Chamomilla*
Chara, *419, *420, 421
Characeae, 14, 24, 418
Chasmogamous flowers, 561
Cheiranthus, *643, *644, 645
Cheirostrobus, 522
Chelidonium, 642 ; mutation, *325 ; seed of, *581
Chemical influences, effect on development, 293
Chemonasty, 358
Chemosynthesis, 254
Chemotaxis, 331
Chemotropism, 352
Chenopodiaceae, 627
Chenopodium, 627
Cherry Laurel, *Prunus laurocerasus*
Chervil, *Chaerophyllum*
Chestnut, *Castanea vulgaris*
Chicory, *Cichorium Intybus*
Chimaeras, 299, *302 ; periclinal, 301
Chiropterophilous plants, 558
Chitin, 38
Chlamydomonas, 398, *399
Chlamydothrix, 376
Chloramoeba, *397
Chlorella, 400, *401
Chlorococcum, 400, *401
Chlorophyceae, 398
Chlorophyll, 18, 250 ; absorption spectrum of, *249
Chloroplasts, 17, 250 ; movements of, 330, *331
Choiromyces, 448
Chondrioderma, *13, 382, *383
Chondriosomes, 16
Chondromyces, *385
Chondrus, *422, 427
Choripetalae, 609
Chromatin, 17
Chromatophores, 11, 17 ; inclusions of, 32 ; multiplication of, 24
Chromoplasts, *20
Chromosomes, 21
Chroococcus, 377
Chroolepideae, 402
Chroolepus, 402
Chrysamoeba, *378, 379
Chrysanthemum, 718
Chrysidella, 380
Chrysomonadinae, 379
Chrysophlyctis, 429
Chrysosplenium, pollination of, 558
Chytridiaceae, 429
Cibotium, 511
Cichorium, *713, 716
Cicuta, *680, 682
Cilia, 328
Cimicifuga, *633
Cinchona, 704, *705, *706
Cincinnus, *129, *130
Cineraria, 718
Cinnamomum, 639, 749
Circaea, 674
Circulation, 13
Circumnutations, 336
Cirsium, 713
Cissus, tendrils, 354
Cistaceae, 647
Cistern epiphytes, 185
Cistiflorae, 646
Citrullus, 709, *710
Citrus, 652, *653, 654
Cladodes, 171
Cladonia, 471, *473, 474
Cladophora, *77, 78, 404, *406 ; cell of, *17, *25 ; chloroplast of, *18 ; polarity, 284
Cladostephus, *79, 409
Cladothrix, *371, 375
Clavaria, *463
Clavarieae, 463
Claviceps, 443, 444 ; sclerotium of, *41
Cleistogamous flowers, 561
Cleistogamy, 561
Clematis, *98, 636
Climbers, anomalous secondary growth, 182
Climbing plants, 182
Clivia, 726
Closterium, 393, *394
Clostridium, 259, 372
Clove, *Eugenia caryophyllata*
Clover, *Trifolium*
Club Mosses, *Lycopodinae*
Cnicus, 713, *714
Cobaea, tendrils, 354
Cocci, 370
Coccolithophoroideae, 380
Cocconeis, 391, *392
Cochlearia, 646

Cocoa tree, *Theobroma Cacao*
Coco-nut Palm, *Cocos nucifera*
Cocos, *739, *740, *741
Coenogametes, 429
Coffea, 704, *707
Coffee plant, *Coffea*
Cohesion, mechanisms, 334 ; theory, 237
Cola, 651
Colchicum, *722, 724, 726 ; seed of, *580
Coleochaete, 404, *405
Collective species, 322
Collema, 474 ; carpogonium, *473
Collenchyma, 61, *62
Colleter, *57, 176
Colletia, 657
Colloidal solutions, 15
Colouring matters, 268
Colours of flowers, 554
Coltsfoot, *Tussilago Farfara*
Columella, 483, 492
Columniferae, 647
Combinations, 325
Comfrey, *Symphytum*
Commelina, 730
Commelinaceae, 730
Commiphora, 655
Companion cells, 158
Compass plant, *Lactuca Scariola*
Compass plants, 351
Compensations, 297
Complementary tissue, 59
Compositae, 711
Conducting tissues, 62
Conduction, 243
Conferva, *397
Conidiospores, 195
Coniferae, 592 ; microspores of, 566
Conium, *678, 682, *683 ; ovary of, *549
Conjugatae, 392
Conjugation in *Spirogyra*, 396
Connecting threads, *44
Connective, 546
Consortium, 469
Contact, stimulus of, 292
Contortae, 687
Contractile roots, 180
Convallaria, *100, *107, 725
Convergence of characters, 174
Convolvulaceae, 691
Convolvulus, 691, 693
Copaifera, 669, 670
Cora, 470, *474
Coralliorrhiza, *191, 256, 746
Corchorus, 649
Cordaitaceae, 604
Cordaites, *604, 605
Cordyline, *143, 725
Corethron, *390, 391
Coriandrum, *678, 683
Cork, *10, 58, *59, *160, *161 ; stone, 58
Cork cambium, 58, 162
Cork cells, 162
Cork oak, 162
Cormophytes, 73 ; gametophyte of, 83
Cormus, 83 ; adaptations of, 165 ; construction of the typical, 84 ; secondary growth in thickness of, 140
Cornaceae, 678
Cornelian Cherry, *Cornus mas*
Cornus, *678
Corolla, 546
Coronilla, 672, *673
Correlation, 296, 310, 314
Corsinia, sporogonium, *480
Cortex, 92
Corydalis, *642, 643 ; seed of, *581
Corylus, 611 ; catkin of, *553
Cosmarium, 393, *394
Cotton, hairs of, 54, *55
Cotton-grass, *Eriophorum angustifolium*
Cotyledons, 117, 565, 575 ; number of, 588
Cowberry, *Vaccinium vitis idea*
Crambe, *643, 646
Crassula, 658
Crassulaceae, 658 ; respiration, 271
Crataegomespilus, 299
Crataegus, 661 ; leaf of, *109, *608
Craterellus, 463
Crenothrix, 371, 376
Crepis, 716
Cribraria, 384
Cribraria rufa, *382
Crinum, 726
Crocus, *728
Crossotheca, *535, 536
Cross-pollination, 201, 558
Croton, 625, 627
Crown-gall, 373
Cruciferae, 643
Crustaceous lichens, 470
Cryptogams, 366
Cryptomeria, 606
Cryptomonadinae, 380
Cryptomonas, *380
Cryptospora, *443
Cucumber, *Cucumis sativus*
Cucumis, 709
Cucurbita, 95, 709 ; pollen-grain of, *36 ; sieve-tubes, *63 ; tactile pits, *353
Cucurbitaceae, 707 ; tendrils, *354
Cupressineae, 596
Cupressus, 597
Cupuliferae, 611
Curcuma, 745
Curvature, 327
Cuscuta, 189, *190, 259, 693
Cuticle, 50
Cutinisation, 38, 39
Cutis tissue, 57
Cutleria, *413, 414
Cutleriaceae, 414
Cuttings, 284

Cyanophyceae, 376
Cyathea, 506
Cyatheaceae, 509
Cyathium, *624, 625
Cycadaceae, 589
Cycadeae, male cells, 562
Cycadeoidea, *605, 606
Cycadinae, 589
Cycadites, 605
Cycas, 589, *590, *591
Cyclamen, *686, 687
Cydonia, 660, 661
Cylindrocystis, *393
Cynara, 713
Cyperaceae, 730
Cyperus, 730, 731
Cypress, *Cupressus sempervirens*
Cypripedium, 746 ; embryo-sac, 572
Cystocarp, 424
Cystodinium, *386, 387
Cystolith, 36, *37
Cystopus, 432
Cytisus, 671, 673
Cytology, 10
Cytoplasm, 11, 15 ; division of, 24 ; inclusions of, 28

Dactylis, 734
Dahlia, 717 ; root-tubers, *178
Dammara, 606
Dandelion, *Taraxacum officinale*
Daphne, 673, *674
Darwinism, 212
Date Palm, *Phoenix*
Datura, 697, *699, 703
Daucus, 682
Day-position, 357
Deadly Nightshade, *Atropa Belladonna*
Death, 220
Deciduous trees, 305
Delesseria, *79, 422, 427
Delphinium, 638 ; ovary of, *547
Dendrobium, 749
Dentaria, bulbils, *194
Dermatogen, 86
Descent, theory of, 206
Desert, 219
Desmidiaceae, 393
Desmids, movements, 328
Desmodium, movement, 337
Determinants, 296, 317
Determination of sex, 314
Deutzia, 659
Development, 217, 278 ; commencement of, 304 ; course of, 301 ; factors of, 288 ; external factors, 288 ; internal factors, 296
Developmental physiology, 278
Diageotropism, 342
Dialypetalae, 629
Dianthus, 627
Diapensia, ovary of, *548
Diastase, 264, 265
Diatomeae, 387 ; Centricae, 389 ; Pennatae, 391 ; movements, 328
Diatoms, *Diatomeae*
Dicentra, 643
Dichasium, 127, *129, *130
Dichogamy, 559
Dichotomosiphon, 407
Dichotomous branching, 119
Dicksonia, 506
Diclinous flower, 545
Dicotylae, 608
Dicotyledons, secondary thickening of, 143 ; systematic arrangement of, 607 ; wood of, 154
Dicranophyllum, 605
Dictamnus, 652
Dictyonema, 474
Dictyostelium, 385
Dictyota, *76, 79, 409, *414, 415 ; growing point of, *80
Dictyotaceae, 415
Diervilla, 706
Diffusion, 224, 243
Digitalis, *702, 703, 704
Dihybrids, 322
Dilatation, 160
Dill, *Anethum*
Dimorpha, *381
Dimorphotheca, 718
Dinobryon, *378, 379
Dinoflagellatae, 386
Dionaea, *187
Dioon, 589 ; fertilisation, 564 ; proembryos, *565
Diospyrineae, 686
Diospyros, 686
Dipsaceae, 706
Dipsacus, 706, *709
Dipterocarpaceae, 647
Dischidia, *184, 690
Discomycetes, 445
Distephanus, *379
Distomatineae, 381
Divergence, 89 ; angle of, 89
Dodder, *Cuscuta*
Dogwood, *Cornus sanguinea*
Dominance, rule of, 321
Dorema, 683
Doronicum, 718
Dorsal suture, 547
Dorstenia, 618
Dracaena, 725, *726, 749
Drepanium, *130
Drimys, 632
Drip-tip, 168
Drosera, *185, *186, 195 ; chemonastic movements, 359
Droseraceae, 639
Drupe, 584

Dryas, 663
Dryobalanops, 647
Drynopteris, *497, 506, *507, *509, 511
Dry Rot fungus, *Merulius lacrymans*
Dudresnaya, 425, *426
Duration of life, 309

Early wood, 153
Ebenaceae, 686
Eeballium, *709
Eccremocarpus, tendrils, 354
Echinocactus, 629
Echinodorus, *720
Echinops, 713
Echium, *694
Ecology, 3; of flower, 551
Ectocarpus, 409, *418
Edelweiss, *Leontopodium*
Egg-cell, 199
Elaeagnaceae, 673
Elaeagnus, 673; nodules, 261
Elaeis, 740
Elaphomyces, 442
Elaphomycetaceae, 442
Elasticity, 60
Elder, *Sambucus*
Elementary species, 322
Elettaria, 745; seed of, *581
Elodea, 721
Elongation, phase of, 284
Embryo, 202, 575
Embryo-sac, 539, *571
Embryonic rudiments, 282
Emergences, 56
Empusa, 435, *436
Enantioblastae, 730
Encephalartos, 589, 606
Enchanter's Nightshade, *Circaea*
Endive, *Cichorium endivia*
Endocarp, 583
Endocarpon, 471
Endodermis, 57, 94, 135
Endophyllum, 459, *460
Endosperm, 565, 580; development of, 574; nucleus, 574
Endospores, 195
Endothecium, 481, 546
Energy, liberation of, 273
Enteromorpha, 402, *403
Entomophilous plants, 553
Entomophily, 556
Entomophthorineae, 435
Enzymes, 264
Ephedra, *602, *603; prothallia, 569
Epidermal system, 49
Epidermis, *49, 92
Epigeal germination, 589
Epigynous flower, *549, 550
Epilobium, 674
Epipactis, 746; cell of, *25
Epiphyllum, 629
Epiphytes, 183, 228
Epipogon, 191, 256, 746
Epithema, 113
Equisetaceae, 502, 517
Equisetinae, 517
Equisetum, *86, *87, 95, 517, *518, *519, *520, 522; germination of the spores of, 290
Ergot, 443, 444
Ergot, *Claviceps purpurea*
Erica, 686
Ericaceae, 684
Ericinae, 684
Erigeron, 716
Eriobotrya, 661
Eriophorum, 730, *731
Erodium, fruit of, 334
Erophila, 646
Erysibaceae, 438, 440
Erysibe, 440, 441
Erysiphe, *27
Erythraea, 689
Erythroxylaceae, 652
Erythroxylon, *652
Escholtzia, 642
Ethereal oils, 30, 268
Etiolation, 289
Eucalyptus, 235, 675, 676
Eucheuma, 428
Eudorina, 399, 400
Eugenia, 675, *676
Euglena, *380, 381
Euglenineae, 380
Eumycetes, 436
Euphorbia, *174, *623, *624, 625, 626
Euphorbia Cyparissias, 294
Euphorbiaceae, 623
Euphrasia, 191, 259, 704
Eurotium, 441
Euryale, 632
Eusporangiatae, 503
Everlasting flowers, *Helichrysum*
Everlasting Pea, *Lathyrus*
Evolution, 2
Excretion of water, causes of, 234
Exine, 541
Exoascaceae, 449
Exoascus, 449
Exobasidiineae, 461
Exobasidium, *460, 461
Exocarp, 583
Exodermis, 135
Exogonium, *693
Exospores, 195
Exothecium, 546
External factors, purposiveness of the reactions to, 295
External segmentation, 71
Extrorse, 546
Exudation, 232, *233
Eye-spots, 20

Fagopyrum, 621 ; achene, *583 ; ovary of, *549
Fagus, 612, *613, *614
False Acacia, *Robinia*
Fascicular cambium, *144
Fats, 30, 266
Fegatella, antheridium, *477
Fennel, *Foeniculum*
Fermentation, 269, 274 ; bacteria of, *373 ; products of, 276
Ferns, *Filicinae*
Ferns, venation of, *500
Fertilisation, 202, 314
Ferula, 683
Festuca, *733, 734 ; flower of, *554
Ficus, 617, *618
Fig, *Ficus carica*
Filago, 717
Filament, 546
Filamentous bacteria, *Trichobacteria*
Filamentous lichens, 470
Filices, 502, 505
Filicinae, 501, 503
Filicinae eusporangiatae, 502
Filicinae leptosporangiatae, 502
Flagella, 328
Flagellata, 378
Flagellates, *Flagellata*
Flax, *Linum usitatissimum*
Floral axis, 549
Floral diagrams, 551
Floral formula, 551
Florideae, 421 ; climbing parts, 356
Flowers, conditions of the formation of, 312 ; morphology and ecology of, 544 ; protandrous, 559 ; protogynous, 559
Foeniculum, *678, 682, 683
Foliaceous lichens, 470
Foliage leaf, diagram of, *109
Follicle, 583
Fomes, *464, 465
Fontinalis, 496
Food materials, assimilation of, 247 ; indispensable, 239
Fool's Parsley, *Aethusa cynapium*
Foreign organisms, effect on development, 294
Forget-me-not, *Myosotis*
Formative tissues, 46
Fossil Angiosperms, 749 ; Gymnosperms, 604
Foxglove, *Digitalis*
Fragmentation, 24
Fragraria, 663
Fragraria monophylla, 325
Frangulinae, 657
Fraxinus, 687, *689
Free cell formation, 26
Free nuclear division, 26
Freycinetia, 737 ; pollination of, 558
Fritillaria, 726
Fruit, 582 ; collective, 582 ; dehiscence of, *583 ; indehiscent, *583 ; partial, 582 ; ripening of, 269 ; spurious, 584
Frullania, 488, *489
Fruticose lichens, 470
Fucaceae, 410, 416
Fucoxanthin, 19
Fucus, 410, *411, *416, *417
Fuligo, 384
Fumaria, nut, *583
Fumariaceae, 643
Funaria, 494, 496 ; archesporium, *481 ; antheridium, *477 ; chloroplasts, *18 ; included starch grains, *24 ; protonema, *476 ; sporogonium, *481
Fungi, nitrogenous food, 258
Funiculus, 539
Funkia, egg apparatus, *572 ; embryos in, *578
Furze, *Ulex*

Galanthus, 726
Galeopsis, *695
Galium, 704 ; schizocarp, *583
Galls, 294, 295, 614 ; histoid, 295 ; organoid, 295
Gametangia, 199, 369
Gametes, 198, 369
Garcinia, 647
Gases, absorption of, 244, 245 ; movement of, 246
Gasteromycetes, 467
Gaultheria, 686
Geaster, 468
Geitonogamy, 201
Gelatinous lichens, 470
Gelidium, 428
Gelsemium, 688
Gemmae, 193, 194
Generative cells, 542, 561
Genes, 317
Genetic spiral, 90
Genista, 671
Gentiana, 688, 689, *690
Gentianaceae, 688
Geographical distribution, 209
Geophytes, 177 ; movement, 327
Geotropic curvatures, 341
Geotropic movement, *341
Geotropic position of rest, alteration of, 344
Geotropism, 339, 340, 346 ; negative, 340 ; a phenomenon of irritability, 346 ; positive, 342
Geraniaceae, 651
Geranium, *651 ; flower of, *552
Germination, 202, 304, 305, 587
Geum, 663
Gigartina, 422, *423, 427
Ginger, *Zingiber officinale*

Ginkgo, 591, *592, 606; male cells, 562; pollen-grain, *562; ovule of, *563
Ginkgoaceae, 591
Ginkgoinae, 591
Girders, 93
Gladiolus, 730
Glandular cells, 70
Glandular epithelium, 70
Glandular hair, *70
Glandular scale, *70
Glandular tissue, 70
Glaucium, *642
Gleba, 468
Glechoma, 696
Gleditschia, 670; stem-thorn of, *174
Gleicheniaceae, 509
Globoid, *31
Gloeocapsa, *40, 377
Glucosides, 29, 268
Glumiflorae, 730
Glycogen, 28
Glycyrrhiza, 672, 673
Gnaphalium, 716
Gnetaceae, 602
Gnetinae, 602
Gnetineae, microspores, 569
Gnetum, 602, *603; embryo-sac, *569
Gooseberry, *Ribes grossularia*
Gossypium, *55, *648, 649
Graft hybrids, 299
Grafting, 297, *298
Gramineae, 732
Grand period of growth, 280
Grape Vine, *Vitis vinifera*
Graphis, 471
Grass-haulm, geotropic erection of, *342
Grass-wrack, *Zostera marina*
Gratiola, *701, 703
Gravity, effect on development, 291
Griffithia, 427
Grindelia, 718
Ground-nut, *Arachis hypogaea*
Growing point, 84, 282, *307
Growth, 217, 278, 306; and cell division, 306; distribution of, 280; grand period of, 280; measurement of, 278; phases of, 282; rate of, 279, 281
Growth in thickness, primary, 140, 286; secondary, 142
Gruinales, 651
Guard cells, 52, 53; movements of, 231
Guiacum, 652
Gum-resins, 268
Gutta-percha, 268, 689
Guttiferae, 647
Gymnadenia, 746
Gymnodiniaceae, 386
Gymnospermae, 589
Gymnosperms, 542; flowers of, 544; secondary thickening of, 143; sexual generation, 561; wood of, 150
Gymnosporangium, *457
Gynaeceum, 546, 547
Gynandrae, 745
Gynostemium, 745
Gyromitra, 447

Haastia, 716
Hadrome, 68
Haemanthus, 726
Haematococcus, 398, *399
Haematoxylin, 158
Haematoxylon, 158, 670
Hagenia, 661, *662, 664
Hairs, 54; scale, *56; stellate, *55; stinging, *57
Halasphaera, 397
Halimeda, 406
Halophytes, 169
Hamamelidaceae, 623
Hamamelidinae, 623
Hamamelis, 623
Hancornia, 689
Haplobacteria, 371, 372
Haplomitrieae, 489
Haplomitrium, *489
Haptotropism, 353
Hart's-Tongue Fern, *Scolopendrium*
Harveyella, 427
Haustoria, *77, 191
Hawthorn, *Crataegus* (*Mespilus*) *oxycantha*
Hay bacillus, *Bacillus subtilis*
Hazel, *Corylus avellana*
Head, 127
Heart-wood, 158
Heat, production of, 276
Heather, *Calluna vulgaris*
Hedera, 678
Hedychium, 745
Helianthemum, *646, 647
Helianthus, *713, 717; embryo-sac of, *575
Helichrysum, 716
Heliotropism, 348
Helleborus, 636; foliage leaf, *119
Helobiae, 719
Hemerocallis, anther of, *541
Hemicelluloses, 37
Hemidesmus, 690
Hemlock, *Conium maculatum*
Henbane, *Hyoscyamus niger*
Hepaticae, 475, 482, 483
Herbs, 141; annual, 180; perennial, 176
Hercogamy, 560
Heredity, 316
Heterocontae, 396
Heteroecious, 458
Heteromerous lichens, 470
Heterophylly, 116, 308
Heterostyly, 560; dimorphic, 560; trimorphic, 560
Heterotrophic cormophytes, 188

Heterotrophic plants, 254
Heterotype division, 205
Heterozygotes, 317
Hevea, 626
Hexoses, 38
Hibernacula, 194
Hibiscus, 649
Hieracium, *713, 716; apospory in, *579
Hilum, 579
Hippocastanaceae, 657
Hippophaë, 673
Hippuris, *87
Histology, 40
Holcus, 734
Holly, *Ilex aquifolium*
Homoiomerous lichens, 470
Homotype division, 205
Homozygotes, 317
Honeysuckle, *Lonicera periclymenum*
Hoodia, 690
Hop, *Humulus lupulus*
Hordeum, 733, 734, *735; apex of a root, *133
Hornbeam, *Carpinus Betulus*
Hornea, 501
Horse-chestnut, *Aesculus hippocastanum*
Horse-tails, *Equisetineae*
Hoya, 690
Humulus, 618, *619
Hyacinthus, 725
Hyaloplasm, 15
Hybrids, 317; inheritance in, 319; in nature, 317
Hydathodes, 71, 168
Hydneae, 463
Hydnophytum, 704
Hydnum, *463
Hydrangea, 659
Hydrastis, *638
Hydrocharis, 194, 721
Hydrocharitaceae, 721
Hydrodictyon, 401
Hydrophilous plants, 553
Hydrophytes, 165
Hydropterideae, 502, 512
Hydrotaxis, 332
Hydrotropism, 352
Hydrurus, 379
Hygrophytes, 167
Hygroscopic movements, 333
Hymenogastreae, 468
Hymenolichenes, 474
Hymenomycetes, 461; clamp connections, 461
Hymenophyllaceae, 509, 510
Hyoscyamus, 697, 699, *701, 703; seed of, *581; stamen of, *547
Hypanthium, 550
Hypericum, 647
Hyphae, *77
Hypholoma, basidium, *452; cell of, *16
Hypnodinium, 387
Hypochnus, 462
Hypocotyl, 565
Hypogeal germination, 589
Hypogynous flower, *549, 550
Hypophysis, 575

Iberis, 646
Ilex, 655, *656
Illicium, 632
Imbibition, 223; mechanisms, 333
Immunity, phenomena of, 295
Indian Hemp, *Cannabis sativa*
Indusium, 508
Inflorescences, 125; diagrams of, *128
Initial cells, 46, *80
Initial layer, 144
Inorganic material, oxidation of, 274
Insectivorous plants, 185, 258
Integuments, 539
Intercellular spaces, 44, 246; lysigenous, 45; schizogenous, 45
Intercellular system, 45
Interfascicular cambium, *144
Internal differentiation, 287
Internodes, 88
Intine, 541
Intramolecular respiration, 272
Introrse, 546
Intussusception, growth by, 35
Inula, 716
Inulin, 28, 265
Iodine, 240
Ipomoea, 693
Iridaceae, 726
Iris, *728, *729, 730; diagram of, *551; seedlings, *588
Irritability, 215
Isatis, 644, 646
Isoetaceae, 502, 530
Isoetes, 523, 530, *531
Isogamy, 198, 369
Isosmotic solutions, 224
Ithyphallus, *468
Ivy, *Hedera Helix*

Jasione, 709
Jasminum, 687
Jateorhiza, 638
Jerusalem Artichoke, *Helianthus tuberosus*
Juglandaceae, 609
Juglandiflorae, 609
Juglans, 609, *610; fertilisation, *574
Juglans regia, chalazogamy, *578
Juncaceae, 721
Juncus, *721
Jungermannia, 489
Jungermanniales, 488
Juniperus, *97, *595, *596, 597, 602

Kandelia, 674 ; seedling, *588
Karyokinesis, 21
Kickxia, 689
Kidney Bean, *Phaseolus*
Kidney-Vetch, *Anthyllis*
Kieselguhr, 392
Klinostat, 340, 350
Knautia, 707
Knight's experiments, 339
Krameria, *668, 670

Labiatae, 694
Laboulbeniaceae, 438, 450
Laburnum, *668, *671, 673
Laburnum Adami, 299, *300
Laburnum, *Laburnum vulgare*
Lachnea, 438, *445
Lactaria, 466, 467
Lactuca, 716
Ladies' Slipper, *Cypripedium*
Laelia, 749
Lagenostoma, *535, 536
Lamarckism, 210
Lamina, 108
Laminaria, 409, *410, *415, 416, 418
Laminariaceae, 409, 416
Lamium, *694, 695
Landolphia, 689
Lappa, *712, 713
Larch, *Larix europaea*
Larix, *600
Late wood, 153
Lateral branches, direction and intensity of growth of the, 125
Lateral branching, 120 ; types of, 125
Lateral buds, position of the leaves of, 122
Lateral root, origin of, *138
Latex, 68, 268
Lathraea, 704
Lathyrus, 672
Laticiferous cells, *68
Laticiferous tubes, 69
Laticiferous vessels, 69
Laudatea, 474
Laurel, *Laurus nobilis*
Laurus, 638, *641
Lavandula, *695, 696
Leaf arrangements, 88 ; alternate, 88 ; main series of, 91 ; verticillate, 88
Leaf axil, 120
Leaf-base, 108, 115
Leaf-blade, 108 ; external form, 109 ; functions of, 114
Leaf-cushions, 115
Leaf mosaic, 115
Leaf, pitchered, *187
Leaf-scars, 119
Leaf-sheath, 108, *116
Leaf-stalk, 108, 115
Leaf-thorns, 172
Leaves, bracteal, 117 ; deciduous, 119 ; development of, 106 ; different forms of, 108 ; duration of life of, 118 ; evergreen, 119 ; foliage, 108 ; internal structure, 111 ; median plane of, 121 ; scale, 117 ; transverse section of, *113 ; venation of, 110
Lecanora, 474
Lecithins, 258, 266
Ledum, 685
Legume, 583
Leguminosae, 664 ; root-tubercles, 260
Lemon, *Citrus limonum*
Lens, 672
Lentibulariaceae, 704
Lenticels, *59
Lentil, *Lens*
Leocarpus, *383
Leontodon, flower-head, *357
Leontopodium, 716
Lepidium, *643
Lepidocarpon, 533
Lepidodendraceae, 503, 533
Lepidodendron, *532, 533
Lepidostrobus, *533
Lepiota, 466
Leptome, 68
Leptosporangiatae, 505 ; antheridia, 510 ; archegonia, 510
Leptothrix, 371
Lessonia, 410
Lettuce, *Lactuca sativa*
Leucin, 258
Leucobryum, 492
Leucojum, 726, *728
Leuconostoc, 373
Leucoplasts, 19, *20, 32, *33
Levisticum, 682
Lianes, 182
Lichen acids, 469
Lichenes, 469
Lichens, *Lichenes*
Licmophora, *388
Life, active, 220 ; conditions of, 218 ; duration of, 309 ; essential phenomena of, 215 ; latent, 220
Light, adaptations for obtaining, 181 ; effect on development, 289 ; production of, 276
Lignification, 38, 39
Ligulatae, 530
Ligule, *116
Ligustrum, 687
Liliaceae, 724
Liliiflorae, 721
Lilium, 725 ; diagram of, *551 ; embryo-sac, 572 ; fertilisation of, *575 ; pollen-grain of, *570
Lilium martagon, germination of, *180
Lime, *Tilia*
Limnanthemum, 689

Limodorum, 746
Linaceae, 652
Linaria, 703
Linnaeus, classification, 365
Linum, *652; gynaeceum of, *548
Liquidambar, 623
Liquorice, *Glycyrrhiza*
Liriodendron, 632
Listera, 746
Litorella, 704, 710
Liverworts, *Hepaticae*
Lobaria, 474
Lobelia, 710, *711; ovary of, *548
Lobeliaceae, 709
Loganiaceae, 688
Lolium, 734, 735, *738
Lonicera, 706
Lophospermum, tendril-like petioles, *355
Loranthaceae, 620
Loranthiflorae, 620
Loranthus, 620
Lotus, *669, 670, 672
Lovage, *Levisticum*
Lunaria, *643
Lupinus, 670, 671
Luzula, 724
Lycoperdon, 467, 468
Lycopersicum, 697
Lycopodiaceae, 502, 524
Lycopodinae, 523
Lycopodinae biciliatae, 524
Lycopodinae pluriciliatae, 524
Lycopodium, *99, 523, *524, *525, *526, 527; bifurcating shoot, *120; stem of, *499
Lygmodendron, *534, *535, 536
Lythrum, 673

Macrocystis, 409, *410
Macrosporangia, 501
Macrospores, 501
Macrozamia, 589
Magnolia, 632
Magnoliaceae, 632
Maianthemum, 725
Main-root, 140
Maize, *Zea mais*
Malacophilous plants, 558
Malva, *647, 648; pollen grain of, *547
Malvaceae, 648
Mammillaria, 629
Mangifera, 655
Mangroves, 167
Manihot, 626
Manures, 244
Maranta, 745
Marantaceae, 745
Marattiaceae, 503
Marcgravia, inflorescence of, *558; pollination of, 556
Marchantia, 484, *485, *486, 487; air-pore, *82; antheridium, *476; archegonium, *478; rhizoid of, *36
Marchantiales, 484
Marsh Marigold, *Caltha palustris*
Marsh plants, intercellular spaces of, 166
Marsilia, *512, *516, *517
Marsiliaceae, 512, 516
Martensia, 423
Mastigamoeba, *381
Matricaria, *712, 713, *715, 718
Matthiola, 645
Maximum, 219
Mechanical influences, effect on development, 292
Mechanical tissue system, 60
Mechanism of development, 278
Mecurialis, 625
Median plane, 72
Medicago, 672
Medick, *Medicago*
Medlar, *Mespilus germanica*
Medullary rays, 95, *146, 156; primary, 146; secondary, 146
Meiosis, 24, 205
Melaleuca, 676
Melampyrum, 191, 704; embryo-sac of, *577
Melica, 734
Melilot, *Melilotus*
Melilotus, 672
Melon, *Cucumis Melo*
Mendel, laws of inheritance, 319
Mendelian rules, validity of, 322
Menispermaceae, 638
Mentha, 696
Menyanthes, 689
Mercurialis, *623
Meringosphaera, 397
Meristems, 46; primary, 46; secondary, 47
Merulius, 465
Mesembryanthemum, 628
Mesocarp, 583
Mesocarpus, chloroplasts, 330
Mesophyll, 112
Mesotaeniaceae, 393
Mespilus, 661
Metabolism, 217, 220
Metals, assimilation of, 262
Metaphase, 23
Metroxylon, 740
Metzgeria, 81, 488, 489; apex of, *82
Miadesmia, 533
Micrasterias, 393, *394
Micrococcus, 374
Microcycas, 589
Micropyle, 539, 579
Microsomes, 15
Microsporangia, 501
Microspores, 501

Mildew fungi, *Erysibaceae*
Milfoil, *Achillea*
Millet, *Andropogon Sorghum*
Mimosa, *664, 667; movements *360; seismonastic movements, 359; state of rigor, 361
Mimosaceae, 664
Mimusops, 686
Minimum, 219
Mirabilis, hybrid, *320
Mistletoe, *Viscum album*
Mitochondria, 16
Mixo-chimaera, 301
Mnium, *83, 491, *493, 494, *495; archegonium, *479; peristome, *496
Modifications, 211, 322
Monarda, 696
Monascus, 438, 439
Monkshood, *Aconitum napellus*
Monoblephrideae, 430
Monoblepharis, *199, 428, *430
Monochasium, 128, *129
Monochlamydeae, 609
Monocotylae, 718
Monocotyledon flower, 559
Monocotyledons, secondary growth in thickness of, 142
Monopodium, 75
Monosporangia, 423
Monotropa, 191, 256
Monstera, 740; perforations, 284
Moraceae, 617
Morchella, *447; hymenium, 439
Morphology, 7; experimental, 9
Morus, 617; inflorescence of, *584
Mosses, *Musci*
Moss-plants, origin of, 475
Movement, 218, 326, 332; conditions of, 329; hygroscopic, 333; nastic, 356; of orientation, 338; paratonic, 337; periodic, 358; of protoplasm, 328; seismonastic, 359; tactic, 329
Movements of curvature, 332; autonomic, 335
Movements of locomotion, 327; mechanism of, 327
Mucilage, 28
Mucilage tubes, 69
Mucor, *434, 435, *436
Mucorineae, 434; heterothallic, 435; homothallic, 435
Mucuna, stem of, *148
Mullein, *Verbascum*
Multicellular formation, 26
Musa, 743
Musaceae, 743
Muscari, 725
Musci, 475, 482, 489
Mutations, 325
Mutisieae 712
Mycelium, 77, *78
Mycobacterium, 373, 374
Mycorrhiza, 191, 256
Myosotis, 694
Myristica, *632; seed, *581
Myristicaceae, 632
Myrmecodia, 704
Myroxylon, *669, *670, 671, 673
Myrtaceae, 674
Myrtiflorae, 673
Myrtle, *Myrtus communis*
Myrtus, 674, *676
Myxamoebae, 383
Myxobacteriaceae, 385
Myxococcus, *385
Myxogasteres, 382
Myxomycetes, 13, 381

Narcissus, 726
Nastic movements, 338, 356
Natural selection, 212
Natural system, 365
Navicula, *391, 392
Nectaries, 71, 550
Nectria, 442
Nelumbium, 632
Nemalion, 424, 427
Neottia, 191, 256, 746
Nepenthaceae, 639
Nepenthes, *187
Nepeta, 696
Nephromium, 474
Nerium, 689, *691
Nerves, 110, 111
Neuropteris, 536
Nicotiana, 697, 699, *700; gynaeceum of, *548
Nicotiana tabacum virginica apetala, 326
Nightshade, *Solanum nigrum*
Nitella, 14, 419, 421
Nitophyllum, 423, 427
Nitrate-bacteria, 254, 274, 375
Nitric acid, assimilation of, 257
Nitrite bacteria, 254, 274, 375
Nitrobacter, *375
Nitrogen, assimilation of, 256
Nitrosomonas, *375
Nodes, 88
Nopalea, 629
Nostoc, *377, 378
Nucellus, 539
Nuclear cavity, 17
Nuclear division, 21, *22; direct, 24; indirect, 21
Nuclear membrane, 17
Nuclear plate, *23
Nuclear sap, 17
Nucleolus, 17
Nucleus, 11, 16
Nuphar, 631
Nutations, 336
Nutmeg, *Myristica fragrans*

Nutrient salts, 237, 243 ; absorption of, 240 ; and agriculture, 243 ; transport of, 242
Nutrient substances, absorption of, 222
Nuts, 583
Nyctinastic movements, 356
Nyctinasty, 357
Nymphaea, *631 ; seed of, *581
Nymphaeaceae, 630

Oak, *Quercus*
Oat, *Avena sativa*
Ocean currents, distribution of seeds by, 586
Ochrea, 116
Ochrolechia, 475
Odontites, 704
Oedogonium, 403, *405
Oenanthe, *681, 682
Oenothera, *674
Oidium, 441
Olea, 687, *688
Oleaceae, 687
Olive Tree, *Olea europaea*
Olpidiopsis, 430
Olpidium, *429
Onagraceae, 674
Ononis, 672
Ontogeny, 2
Oogonium, *199, 369
Oomycetes, 430
Oosphere, 199, 369
Ophiocytium, 397
Ophioglossaceae, 504
Ophioglossum, *504, *505
Ophrys, 746
Opium Poppy, *Papaver somniferum*
Optimum, 219
Opuntia, *173, 628, 629
Orchidaceae, 745
Orchis, *746, *747, *748 ; root-tuber, *179
Organic acids, 28, 268
Organic bases, 258
Organography, 71
Organs, 71 ; vegetative, 73
Origin of species, 316
Ornithogalum, *723, 725
Ornithophilous plants, 557
Ornithophily, 556
Ornithopus, 672
Orobanchaceae, 704
Orobanche, 191, *703, 704
Orthostichies, 89
Orthotropous, 72, 123
Oryza, 734, 735, *736
Oscillaria, *377
Osmometer, 224
Osmosis, 224
Osmotic pressure, 224 ; high, 227
Osmunda, *509
Ostrich Fern, *Struthiopteris germanica*
Ourouparia, 705
Ovaries, transverse sections of, *548
Ovules, 198, 539, 540 ; position of, 549
Ovum, 567
Oxalis, movement, 337
Oxygen, 244 ; evolution of, *248

Padina, 415
Paeonia, 638 ; flower of, *197, *545
Palaeontology, 209
Palaeostachya, *521, 522
Palaquium, *685, 686
Palisade cells, 112
Palmae, 738
Pandanaceae, 737
Pandanus, 737, *741
Pandorina, 399
Panicle, 126, *127
Panicum, 734
Pantostomatineae, 381
Papaver, 95, *642, 643 ; seed of, *581
Papaveraceae, 640
Papilionaceae, 670
Papillae, *54
Parasites, 188, 255, 256, 259
Parastichies, 90, *91
Paratonic movements, 337
Parenchyma, 48 ; assimilatory, 49 ; conducting, 49 ; water-storage, 49
Paris, 725, 726, *727
Parmelia, *471, *472
Parnassia, 659
Parsley, *Petroselinum*
Parsnip, *Pastinaca*
Parthenocissus, *182, 658 ; tendrils, 355
Parthenogenesis, 193, 316, 577
Partial parasites, 191
Passiflora, ovary of, *548 ; tendrils, 354
Pastinaca, 682
Paullinia, 655
Pavetta, 704
Payena, 686
Pea, *Pisum*
Pea, reserve material, *580
Peach, *Prunus persica*
Pear, *Pyrus communis*
Pectic substances, 38
Pediastrum, 401, *402
Pedicularis, 191, 259, 704
Peireskia, 628
Pelargonium, *651
Pellia, 488, 439
Peltigera, 472, 474
Penicillium, *78, 441
Pentacyclicae, 684
Pentosanes, 37
Perception, 338
Perianth, 545
Periblem, 86
Pericarp, 583

Perichaetium, 492
Periclinal cell walls, 307
Pericycle, 95, 136
Periderm *160, 162
Peridineae, 386
Peridiniaceae, 386
Peridinium, *386, 387
Perigone, 546
Perigynous flower, *549, 550
Periodicity, 304
Periplasm, 500
Perisperm, 581
Peristome, 495
Perithecium, 439
Periwinkle, *Vinca minor*
Peronospora, *77, *433
Peronosporeae, 431
Persea, 639, *640
Personatae, 696
Petals, 197
Petasites, 718
Petiole, 108
Petroselinum, 682
Petunia, *697
Peziza, *445
Phaeocystis, 380
Phaeophyceae, 409
Phaeosporeae, 412
Phaeothamnion, 380
Phalloideae, 468
Phallus, 468
Phascum, 496
Phaseolus, 673; pulvinus of, *337
Phelloderm, 162
Phellogen, 162
Phelloid tissue, 59
Philadelphus, 659
Phleum, 734
Phloem, 68
Phobophototaxis, 330
Phoenix, 740
Phormium, *112
Phosphorescence, 277
Phosphoric acid, assimilation of, 262
Photonasty, 357
Photosynthesis, 254
Phototaxis, 330
Phototropic perception, localisation of, 351
Phototropism, 348, *349, 351; a phenomenon of irritability, 351; transverse, 350
Phragmidium, 455, 456, 457, *458, *459, 460
Phycocyan, 19, 423
Phycoerythrin, 19, 423
Phycomyces, 435
Phycomycetes, 428
Phycoxanthin, 411
Phyllactinia, 440, 441
Phyllocactus, 629
Phylloclades, 171
Phylogeny, 2
Physalis, fruit of, *584
Physarum, *384
Physiology, 215; object of, 215
Physostigma, 673
Phytelephas, 740
Phyteuma, 709
Phytolacca, 95
Phytopathology, 303
Phytophthora, 431, *432
Picea, *599, 600; embryo, *568; ovule of, *567
Picorhiza, 704
Picrasma, 654
Pilobolus, 434; phototropism, 349, *350
Pilocarpus, 654
Pilostyles, *189
Pilularia, *512, 516, 517
Pimenta, 676
Pimpinella, *678, 681, 683
Pinaceae, 593, 596
Pine, radial section, *152; tangential section, *153; transverse section, *151
Pinguicula, 186, 704
Pinnularia, *74
Pinus, 600, *601, 602, 606; archegonium of, *567; embryo, *568; germination, *587; male flower, *544; pollen-tube, *566
Piper, 95, *622, 623
Piperaceae, 621
Piperinae, 621
Pistacia, 655
Pisum, 672
Pith, 95
Pithecoctenium, winged seed of, *585
Pits, *35, *42, *43; bordered, 65; tactile, 353
Pitting, 43
Placenta, 539, 547
Placentation, axile, 548; free central, 548; parietal, 548
Plagiochila, 80, *81, *488, 489
Plagiogeotropism, 342
Plagiotropous, 72, 123
Plankton, 74
Planktoniella, *388
Plant geography, 244
Plantaginaceae, 704
Plantago, 704; inflorescence of, *559
Plantain, *Plantago*
Plants, chemical composition of, 220; organs of, 71; perception in, 338; sensation in, 338; size of, 281; stability of, 60
Plasmodesms, *44
Plasmodiophora, 385
Plasmodiophoraceae, 385
Plasmodium, 13, 382
Plasmolysis, *226

Plasmopara, 432, 433
Plastids, 11
Platanaceae, 623
Platanthera, 746
Platanus, 623
Platystemon, 642
Plectascineae, 441
Plectonema, *78
Pleiochasium, 127
Plerome, 86
Pleuridium, 496
Pleurocarpi, 496
Pleurocladia, *412
Pleurosigma, 391, 392
Plum, *Prunus domestica*
Plumbagella, embryo-sac, 572
Plumeless Thistle, *Carduus*
Plumule, 565
Pneumatophores, 167, 246
Poa, 734
Pocket-leaves, 185
Podetium, 471
Podocarpus, 593; mycorrhiza, 261
Podophyllum, 638, *639
Podospora, 442; perithecium, *443
Podostemaceae, 576
Poisons, 294
Polarity, 72, 282, 291, *292, 305; establishment of, 74
Pollen-chamber, 563
Pollen grains, 197, 540
Pollen sacs, 197, 540, 546; cohesion mechanisms, 335; development of, 541
Pollen-tube, 201, 541
Pollination, 201, 545; of flower, 551
Polyangium, *385
Polycarpicae, 629, 639
Polygala, *655
Polygalaceae, 655
Polygamy, 546
Polygonaceae, 621
Polygonatum, *719, 725, 726; geotropism, *345; rhizome of, 119
Polygoninae, 621
Polygonum, *621; embryo-sac in, *571; ovary of, *572
Polyhybrids, 322
Polypodiaceae, 508
Polypodium, 507, 509, *511
Polyporeae, 463
Polyporus, 465, 467
Polysiphonia, 427
Polytoma, *399
Polytrichaceae, 495
Polytrichum, *491, 492, 494, 496; antheridium, *479
Pond-weed, *Potamogeton natans*
Poplar, *Populus*
Populus, 615, *616
Porogamy, 573
Potamogeton, *720, 721
Potamogetonaceae, 721
Potentilla, 663
Presentation-time, 348
Primula, *686, 687; heterostyled flowers, *560
Primulaceae, 687
Primulinae, 687
Pro-embryo, 565, 568, 575
Promycelium, 455
Prophase, 23
Prop-roots, 140
Prosenchyma, 48
Protandry, 559
Proteid crystals, 30
Proteids, hydrolysis of, 267
Prothallium, 567
Protococcales, 400
Protogyny, 559
Protomastiginae, 381
Protonema, 475, *476, 490
Protoplasm, 218; movements of, 13, 326, 328; permeability of, 241
Protoplasts, 11; chemical properties of, 14; connections of, 43; inclusions of, 27; main vital phenomena of, 13; origin of the elements of, 21; structure of the parts of, 15
Prunus, *107, *660, *663, 664
Psalliota, *464, 466
Pseudo-parenchyma, 437
Pseudotsuga, 598
Psidium, 675
Psilophytales, 501
Psilophyton, 501
Psilotaceae, 502, 527
Psilotum, 527
Psychotria, 704, 705
Pteridium, *498, 509
Pteridophyta, 496; classes of, 501; embryo, 498; gametophyte, 497; heterosporous, 501; homosporous, 501; prothallium, 497; sexual reproduction, 200; sporangia, *197, 499; spores, 499; sporophylla, 499; sporophyte, 498; suspensor, 498; vascular bundles, 499; vascular system, 105
Pteridospermeae, 503, 534
Pteris, *101; apex of a root, *132; embryo, *497
Pterocarpus, 673
Ptyxis, 87
Puccinia, *456, *457, 458, 459
Pulvinus, *115, 336, *337, 351
Pumpkin, *Cucurbita Pepo*
Punica, 676, *677
Punicaceae, 676
Pure line, 322
Pycnidia, 443
Pycnoconidia, 443
Pycnospores, 443

Pyrenoids, 18
Pyrenomycetes, 442
Pyronema, 438, 439, 445, *446, *447
Pyrus, 660, 661; flower, *550
Pythium, 433

Quassia, 654, *654
Quercifloræ, 609
Quercus, *614, *615, 749; cupule, *613
Quillaja, 660, 664
Quince, *Cydonia vulgaris*

Raceme, *126
Radial vascular bundle, 136
Radicle, 565
Radish, *Raphanus sativus*
Rafflesia, 189
Rafflesiaceæ, 639
Ramalina, 471
Ramenta, 54
Ranunculaceæ, 633
Ranunculus, *633, *634, *635, 636; flower, *550; root of, 136; vascular bundle, *104
Raoulia, *170, 716
Raphanus, 646
Raphe, 579
Raphides, 30, *31
Raspberry, *Rubus idæus*
Ravenala, 745
Reaction-time, 347
Receptacle, 508
Red Algæ, *Rhodophyceæ*
Red Currant, *Ribes rubrum*
Reduction division, 24, 203, *206, 369
Regeneration, 164, 282; in Bryophyta, 481
Regulation, capacity of, 217
Reindeer Moss, *Cladonia rangiferina*
Rejuvenation, 21
Reparation, 282
Reproduction, 192, 217, 310; asexual, 193; conditions of, 311; digenetic, 193; monogenetic, 193; sexual, 193, 315; organs of, 192; vegetative, 193
Reseda, multicellular formation, *26
Reserve materials, 263; mobilisation of, 263; regeneration of, 268; transport of, 267
Resins, 30, 268
Respiration, 269, 273; experiment to demonstrate, *271; intramolecular, 272
Respiratory coefficient, 270
Respiratory roots, *167
Rest-Harrow, *Ononis*
Resting condition, 303; awakening from, 305
Restitution, 164, 282; stimulus of, 305
Rhabdonema, 392
Rhamnaceæ, 657
Rhamnus, *657, 658
Rheum, *621
Rhinanthus, 191, 259
Rhipidium, *130
Rhipsalis, 629
Rhizoids, 80
Rhizomes, 177
Rhizomorphs, 466
Rhizophora, *168, 674, *675
Rhizophoraceæ, 674
Rhizopus, *433, 434, 435
Rhododendron, 685; ovary of, *548
Rhodomela, 427
Rhodophyceæ, 421
Rhoeadinæ, 639
Rhubarb, *Rheum*
Rhus, 655
Rhynia, 501
Ribes, *659
Riccia, 80, *81, *487
Ricciaceæ, 487
Rice, *Oryza sativa*
Richardia, 740
Ricinus, *625, *626, 627; endosperm of, *31
Rigidity against bending, 93, *94
Rigor, 361
Robinia, *174, 672
Roccella, 471, 475
Rock Rose, *Helianthemum vulgare*
Root-cap, 131
Root-climbers, 182
Root-hairs, *54, 134, *134, *227
Root-pockets, 131
Root-pressure, *234, 236
Root-system, appearance of, 139
Root-thorns, 172
Root-tubercles, *260
Root-tubers, 179
Roots, 131, 139; borne on shoots, 139; branching of, 138; external features of, 132; geotropic curvature of, *342; growing point, 131; growth in thickness of, *147; mechanical tissue of, *137; primary structure of, 134
Rosa, *660, 664; fruit of, *582
Rosaceæ, 660
Rose of Jericho, *Anastatica hierochuntica*
Rosiflorae, 658
Rosmarinus, 696
Rotation, 13
Rowan, *Sorbus* (*Pyrus*) *aucuparia*
Royal Fern, *Osmunda regalis*
Rozites, 467
Rubia, 704
Rubiaceæ, 704
Rubiinæ, 704
Rubus, 663; collective fruit of, *584
Rumex, 621
Runners, 194
Ruppia, 721
Ruscus, cladode, *173
Rush, *Juncus*

Russula, *461, 467
Rust Fungi, *Uredineae*
Rust of Wheat, *Puccinia graminis*
Ruta, 652, *653
Rutaceae, 652
Rye, *Secale cereale*

Sabadilla, 725
Saccharomyces, *27, 449, *450
Saccharomycetes, 449
Saccharum, 734
Saffron, *Crocus sativus*
Sagittaria, 719, *720, 721
Salicaceae, 614
Salicifloræ, 614
Salicornia, *173
Salix, 615, *616
Salvia, *696 ; pollination of, 555, *556
Salvinia, *513, *514, *515
Salviniaceae, 512, 513
Sambucus, 706 ; flower of, *547
Sanguisorba, *660, 661
Santalaceae, 620
Santalum, 620
Sapindaceae, 655
Sapindinae, 655
Saponaria, 627, *629
Sapotaceae, 686
Saprolegnia, *35, 430, *431 ; course of development of, 311 ; zoospores, *196
Saprolegniaceae, 430
Saprophytes, 255, 256
Sarcina, 375
Sargassum, 410
Sarothamnus, 671
Sarraceniaceae, 639
Sassafras, 638, *640
Savannahs, 219
Saxifraga, 659
Saxifragaceae, 659
Saxifrage, *Saxifraga*
Scabiosa, 707
Scalariform pitting, *66
Scale leaves, 118
Scandix, 682
Scenedesmus, 401, *402
Schistostega, *493, 496
Schizaeaceae, 509
Schizocarp, 584
Schizonema, 388
Schizosaccharomyces, 449
Schoenocaulon, 725
Sciadium, 397
Sciadopitys, 598
Scilla, 725
Scinaia, 427
Scirpus, 730, *731
Scitamineae, 742
Sclerenchyma, 60, *62
Sclerenchymatous fibre, *61
Scleroderma, 467, 468
Scleropodium, *493
Sclerospora, 433
Sclerotium, 437
Scolopendrium, *508
Scorzonera, 716 ; seedlings, *588
Scrophulariaceae, 703 ; floral diagrams of, *208
Scurvy Grass, *Cochlearia officinalis*
Sea lettuce, *Ulva lactuca*
Secale, 733, 734, *735
Sedum, 658, *659
Seeds, 193, 540, 579 ; distribution of, 584
Segregation of characters, 320
Seismonasty, 359
Selaginella, 523, 527, *528, *529, *530
Selaginellaceae, 502, 527
Selection, 324
Selective power, 241
Self-pollination, 201
Self-sterility, 558
Semi-permeable membrane, 224
Sempervivum, 658 ; formation of the flowers of, 312
Senecio, 711, 718
Sensitive Plant, *Mimosa pudica*
Sepals, 197
Sequoia, 235, 598, 599, 606
Serjania, *183
Sex, determination of, 314
Sexual reproduction, significance of, 315
Sexual reproductive cells, 198
Shaddock, *Citrus decumana*
Shade plants, 181
Shepherd's purse, *Capsella bursa pastoris*
Shoot-thorns, 172
Shoots, 84 ; adventitious, 122 ; aerial, 84 ; axillary, 121 ; branching of, 119 ; endogenous, 122 ; formed from roots, 306 ; normal, 122 ; order of sequence of, 124 ; subterranean, 84
Shorea, 647
Shrubs, 141
Sieve-pits, 63, *64
Sieve-plates, 63, 159
Sieve-tubes, *63, *64, 158
Sigillaria, 532
Sigillariaceae, 502, 532
Silene, *630
Siler, *678
Siliceous earth, 392
Silicoflagellatae, 380
Silicon, 240
Silver Fir, *Abies pectinata*
Simarubaceae, 654
Sinapis, 645
Siphonales, 405
Siphonocladiales, 404
Siphonocladus, 404
Siphonogams, 542
Sisymbrium, *644
Sium, 682

Sleep-position, 357
Sliding growth, 48, *150
Slime fungi, *Myxomycetes*
Smilax, 725, 749
Smut Fungi, *Ustilagineae*
Sodium, 240
Soil, power of absorption of, 242
Solanaceae, 696
Solanum, 696, *697, 699 ; tuber, *177
Solerina, 474
Solidago, 716
Sols, 15
Sonneratia, *167
Sorbus, *660, 661 ; hybrid, *318
Soredia, 471
Sorrel, *Rumex acetosa*
Spadiciflorae, 737
Spanish Pepper, *Capsicum annuum*
Sparassis, 463
Sparganiaceae, 737
Spartium, 672, 673
Species, 322 ; origin of, 206, 326
Spermatogenous cell, 561
Spermatophyta, 539, 542 ; sexual reproduction, 200
Spermatozoids, 199, 369, 565 ; chemotaxis, 331 ; of *Zamia*, *563
Spermogonia, 455
Sphaeria, 442
Sphaerococcus, 427
Sphaero-crystals, 34
Sphaeroplea, 404
Sphaerotheca, 440, 441
Sphagnales, 493
Sphagnum, *490, 493
Sphenophyllaceae, 502
Sphenophyllinae, 522
Sphenophyllum, *522
Sphenopteris, 536
Sphere-crystals, 28
Spike, *126
Spinach, *Spinacia oleracea*
Spinacia, 627
Spiraea, *660
Spirillum, 370, *371
Spirodinium, 387
Spirogyra, 395, *396 ; cell of, *25
Spirophyllum, 376
Spirotaenia, 393
Splachnum, 494
Splint-wood, 158
Spongy parenchyma, 113
Sporangial spores, 195
Sporangium, 195, *509 ; cohesion mechanisms, 334, *335
Spores, 193, 195, 369
Sporidium, 455
Sporodinia, 434, *435
Sporogonium, 196 ; hygroscopic movements, 334
Sporophylls, 197
Sporothecae, 501
Spring wood, 153, 154
Stachys, 695
Stamens, 197, 540, 546
Staminodes, 546
Stangeria, 589
Stapelia, *174, 690 ; pollination of, 556
Staphylococcus, 374
Starch, 32, 252, *253, 264 ; assimilation, 32 ; reserve, 32
Starch grains, *33
Starch sheath, 94, 102
Statolith-hypothesis, 347
Statoliths, 346
Stelar theory, 106
Stele, 106
Stellaria, 627
Stem, primary internal structure of, 92
Stemonitis, *382, 384
Stem-tendrils, 182, *182
Stem-tubers, 177
Sterculiaceae, 650
Stereome, 60
Stereum, 463
Stigma, 201, 548
Stigmatomyces, *450
Stimulus, 337 ; conduction of, 361 ; movements, 337
Stinging Nettles, *Urtica*
Stink-horn, *Ithyphallus impudicus*
Stipa, section of the leaf, *172
Stipules, 108
Stock, *Matthiola*
Stomata, 51, *52, 230, 231, *246
Stomatal apparatus, 51, 52, *53
Stoneworts, *Characeae*
Storage parenchyma, 148
Stratification, *35, 41
Stratiotes, 194, 721
Strawberry, *Fragraria*
Strelitzia, 745 ; ornithophilous flower of, *557 ; pollination of, 556
Streptochaeta, 732
Streptococcus, 373, *374
Striation, *371
Strickeria, *443
Strophanthus, 689, *692
Struggle for existence, 212
Struthiopteris, 508 ; spermatozoid, *510
Strychnos, 688, *689
Style, 548
Styracaceae, 686
Styrax, 686
Suberisation, 38, 39
Subtending leaf, 121
Succisa, 707, *709
Succulent stems, *174
Suction force, 237
Sugar-cane, *Saccharum officinarum*
Sugars, 28
Sulphur bacteria, 254, 274, 376

Sulphuric acid, assimilation of, 261
Sunflower, *Helianthus annuus*
Surirella, 391
Suspensor, 565,-575
Swarm spores, 196
Swertia, 689
Symbiosis, 469
Symmetry, 282, 306; dorsiventral, 75; planes of, 72; relations of, 72
Sympetalae, 684
Symphytum, 694
Sympodium, 127
Synandrae, 707
Syncarpous gynaeceum, 547
Synchytrium, 429
Synedra, 392
Syringa, 687, *687

Tabernaemontana, 689
Tactile pit, *353
Taeniophyllum, *175
Tamarindus, *666, *667, *668, 669, 670
Tannin, 29, 268
Tapetum, 500
Taphrina, *449
Tap-root, 140
Taraxacum, 712, 713, *714, 718; modifications, *323
Taxaceae, 598
Taxodium, 596, *597, 606
Taxus, *97, *593, *594, 602; embryo-sac, *566
Teak-tree, *Tectona grandis*
Teazel, *Dipsacus*
Tectona, 694
Teleutospores, 455
Telophase, 23
Temperature, effect on development, 288
Tendril climbers, 182
Tendrils, *181, 182, 353; points of reversal, 354
Teratology, vegetable, 303
Terfezia, 442
Terfeziaceae, 442
Terminal bud, 121
Ternstroemiaceae, 647
Tetracyclicae, 687
Tetraspores, 423
Teucrium, 695
Thalictrum, 95
Thallophyta, 367; phylogenetic connections of, 368; reproduction of, 369; sexual reproduction, 198
Thallus, 73; internal structure of, 78
Thamnidium, 435
Thea, *646
Thecotheus, 439
Thelephoreae, 463
Theobroma, *649, *650, 651
Theory of descent, 1, 206, 326
Thermonasty, 356
Thesium, 191, 259, 620
Thigmotropism, 353
Thorn-apple, *Datura Stramonium*
Thorns, 171
Thuja, 596, 597; germination, *587
Thyloses, 158
Thymelaeaceae, 673
Thymus, 696
Tilia, *649; radial section of the wood of, *157; tangential section of the wood of, *156; transverse section of the bast of, *159; transverse section of a stem of, *154: transverse section of the wood of, *155
Tiliaceae, 649
Tillandsia, 185
Tilletia, *454
Tilletiaceae, 454
Tilopteridaceae, 414
Tissue-systems, 45
Tissue tensions, 286, *287
Tissues, boundary, 49; formation of, 40; permanent, 47
Tmesipteris, 527
Tobacco, 697
Tolypellopsis, 421
Tone, alteration of, 345, 351
Toothwort, *Lathraea squamaria*
Topophototaxis, 330
Torsion, 91
Tozzia, 191, 259, 704
Tracheae, 64, *65; annular, 65; reticulate, 65; spiral, 65
Tracheides, 64, *65; annular, 65; reticulate, 65; scalariform, *66; spiral, 65
Tradescantia, *14, 730
Tragopogon, 716
Transpiration, 228; cuticular, 230; stomatal, 230
Transpiration stream, 235
Transverse geotropism, 342
Trapa, 674
Tree-ferns, 506
Trees, 141; longevity of, 310
Tremella, basidium, *452
Tremellineae, 460
Trentepohlia, 402
Tribonema, 397
Trichia, *383
Trichobacteria, 371, 375
Trichocaulon, 690
Trichogyne, 424
Tricholoma, 466
Trichomanes, *510
Tricoccae, 623
Trifolium, 672; movement, 337
Trigonella, 672
Triticum, 733, 734, *735; endosperm, *31
Tropaeolum, chromoplasts, *20
Tropisms, 338
Tropophytes, 175

Truffles, *Tuberaceae*
Trypanosoma, *381
Tuberaceae, 447
Tubers, 178, 194, 308, 447 *448
Tubiflorae, 690
Tulipa, 725; bulb, *178
Turgescence, *225
Turnip, *Brassica napus*
Tussilago, *716, 718
Twining plants, 182, 343, *344
Typhaceae, 737
Tyrosin, 258

Ulex, 672
Ulmaceae, 616
Ulmus, 616, *617; development of the leaf, *108; ovule of, *573
Ulothrix, *199, 402, *404
Ulotrichales, 401
Ulva, *75, 402
Umbel, *127
Umbelliferae, 679
Umbelliflorae, 677
Uncinula, 440, *441
Unfolding buds, distribution of, 124
Unicellular bacteria, *Haplobacteria*
Uragoga, 705, *708
Uredineae, 455
Uredospores, 457
Urginea, *723, 725, 726
Urtica, 619; hybrid, *321
Urticaceae, 619
Urticinae, 616
Usnea, 471, *472
Ustilaginaceae, 453
Ustilagineae, 452
Ustilago, *453, 454, *455; brand-spores, 453
Utricularia, *186, 704

Vaccinium, 685, *685
Vacuoles, 12
Valerian, *Valeriana*
Valeriana, 706, *708
Valerianaceae, 706
Vallisneria, 721
Vanda, 749
Vanilla, *747, 748
Variability, 316, 322
Variation curves, *324
Vascular bundles, arrangement, 95; bicollateral, 100; cauline, 96; collateral 100; common, 96; complete, 67; concentric, 99, *100, *101; course of, 96; foliar, 96; incomplete, 67; radial, 99; structure of, 99; system, 67; system of tissue of, 67; termination of, *111
Vascular cryptogams, 496, 499
Vascular plants, 366
Vascular system, phylogeny of, 105
Vaucheria, *407, *408
Vegetable kingdom, phylogeny of, 365
Vegetative cone, *85, *86, *87
Vegetative form, periodic changes in, 307
Veins, 110
Velamen, 184
Velum, 465
Venation, 110
Ventral canal-cell, 567
Ventral suture, 547
Veratrum, 725, 726
Verbascum, *701, 703
Verbena, *694
Verbenaceae, 694
Vernation, 87
Veronica, 703
Verrucaria, 471
Vessels, 64, 148; pitted, 65; scalariform, 65
Vetch, *Vicia*
Vibrio, 370, *371, 374
Viburnum, 705, 706
Vicia, *668, 672, 673
Victoria, 632
Vinca, 689, *690
Vincetoxicum, 690, *693
Viola, *646; capsule, *583; flower of, *552
Violaceae, 647
Viscaria, *630; diagram of, *551
Viscum, 192, 259, 620, *620
Vitaceae, 658
Vitis, *658
Viviparous plants, 589
Volva, 465
Volvocales, 398
Volvox, 399, *400

Wall, growth in thickness, 36
Wallflower, *Cheiranthus Cheiri*
Walnut, *Juglans regia*
Water, 222; absorption of, 223, 227; assimilation of, 262; conduction of, 235; movement of, 228
Water cultures, 238, *239
Water-Ferns, *Hydropterideae*
Water-Hemlock, *Cicuta*
Water-net, *Hydrodictyon*
Water Nut, *Trapa*
Water-Parsnip, *Sium*
Water plants, 165, 228
Water-pores, *114
Water-stomata, 113, 233
Water-storage tissue, 113
Wax incrustation, *50
Weigelia, 706
Welwitschia, 108, *602; prothallia, 569
Wheat, *Triticum*
White Mustard, *Sinapis alba*
White Water Lily, *Nymphaea alba*
Whorl, 88

Wild Cabbage, *Brassica oleracea*
Wild Cherry, *Prunus cerasus*
Willoughbeia, 689
Willow, *Salix*
Willow-herb, *Epilobium*
Wind-dispersal, seeds, 585
Winter buds, *176
Wistaria, 672, 673
Witches'-brooms, 449
Wood, 148; arrangement of the tissues in, 151; autumn, 153; grain of, 157; heart-, 158; splint-, 158; spring, 153; subsequent alterations of, 157
Wood-fibres, 148
Wood parenchyma, 149
Woodsia, antheridium, *510
Wormwood, *Artemisia Absinthium*
Wounds, healing of, 164

Xanthophyll, 19
Xenogamy, 201
Xerochasy, 333
Xeromorphy, 169
Xerophytes, 168
Xylem, 68

Yeast Fungi, *Saccharomycetes*
Yeast fungus, fermentation, 275
Yew, *Taxus baccata*
Yucca, 725; pollination of, 556

Zamia, 589; fertilisation, *565; formation of spermatozoids in, *562; spermatozoids, *563
Zanardinia, 414
Zanichellia, 721
Zea, *92, 734, 735; vascular bundle, *102, *103
Zingiber, *744, 745
Zingiberaceae, 745
Zoosporangia, 196
Zoospores, 196, 369
Zostera, 721
Zygnema, 395
Zygnemaceae, 395
Zygogynum, 632
Zygomorphic, 72
Zygomorphic flowers, geotropic orientation of, 343
Zygomycetes, 434
Zygophyceae, 393
Zygophyllaceae, 652
Zygosaccharomyces, 449
Zygospore, 199, 369, 434
Zygote, 199, 369
Zymase, 275

THE END

Printed by R. & R. Clark, Limited, *Edinburgh*.